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The Interaction of Ultraviolet-B Radiation Stress and Plant Competition in Agricultural Plant Populations

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THE INTERACTION OF ULTRAVIOLET-B RADIATION STRESS AND PLANT COMPETITION IN AGRICULTURAL PLANT POPULATIONS

by

Warren Glenn Gold

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of

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Warren G. Gold

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ABSTRACT

The Interaction of Ultraviolet-B Radiation
Stress and Plant Competition in
Agricultural Plant Populations

by

Warren Glenn Gold, Master of Science
Utah State University, 1983

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Department: Range Science

The effect of ultraviolet-B radiation enhancement upon the competitive interactions of two species pairs was studied in the field. Wheat (*Triticum aestivum* L. 'Bannock') was paired with wild oat (*Avena fatua* L.) and jointed goatgrass (*Aegilops cylindrica* Host) to represent competition between species pairs in agricultural situations. Specially modulated ultraviolet lamp systems provided either low ultraviolet-B enhancement (simulation of a 16 % ozone layer reduction based upon the generalized plant action spectrum), high ultraviolet-B enhancement (40 % ozone reduction) or control (ambient solar ultraviolet-B) irradiance.

Ultraviolet-B radiation enhancement significantly altered the competitive interactions of the species pairs. However, ultraviolet-B enhancement did not affect total shoot biomass production in the mixtures or shoot biomass production of the species in monoculture. The direction in which competitive interactions were altered appeared to be dependent upon the time at which the seeds were planted. Also, water stress affected some aspects of the interaction between ultraviolet-B enhancement and plant competition but the manner of this effect was inconsistent. Reproductive effort of the species was generally not affected by ultraviolet-B enhancement, except in wild oat plants under interspecific competition.

(71 pages)

INTRODUCTION

Environmental stresses often impose constraints upon the vegetative and/or reproductive production of higher plants. These stresses can take the form of either shortages or excesses of environmental factors that affect plant production (e.g. water, nutrients, solar radiation). These stresses can act directly (e.g. by affecting the actual photosynthetic carbon gain ability of the plant) or indirectly (e.g. through increasing energetic demands to facilitate survival in a stressful environment). In addition, plants under natural conditions are usually subject to many different types of stresses (biotic and abiotic) which often interact with each other. Thus, plants in the field are exposed to a complex of environmental stresses which affect plant growth and survival rather than a set of isolated stresses. The nature of this stress complex incident upon a plant may change through time since the relative importance of individual stresses and the interrelationships among stresses change within and between growing seasons (e.g. Bjorkman 1981).

The plasticity, or acclimation potential of a plant to a change in the current suite of environmental pressures, is a genotypically-controlled, species-specific characteristic. Thus, an alteration of any specific environmental stress could lead to changes in the competitive situation of a plant community through the differential tolerance of the competing species to that change. This change in the competitive status of certain species could further alter the productivity of those species (Grime 1977, 1979).

In addition to the potential alteration of competitive interactions by an environmental stress, plant competition (as well as other stresses) can alter both the form and degree of the physiological manifestation of a particular environmental stress. Many studies on plant response to a changing environmental stress have either isolated plants from all other stresses present in the natural environment or held such stresses constant. This allows an examination of the physiological response to that stress alone, but has limited value in predicting the response to a change in that stress under natural conditions. For example, Mueggler (1972) showed that the effect of clipping on Agropyron spicatum is dependent upon the intensity of plant competition present. Lee and Bazzaz (1980) also found a significant interaction between competitive intensity and response to defoliation in Abutilon theophrasti. Teramura et al. (1980) have shown that the effect of ultraviolet-B radiation on soybeans is highly dependent upon the visible radiation environment. These and many other studies indicate that factor interaction has an important influence upon a plant's response to its environment. Thus, the presence of plant competition and other natural stresses are necessary to allow the interpretation of the effect of any particular environmental stress in an ecological context.

In a unique experiment, Austin and Austin (1980) examined both the ecological response (competition present) and the physiological response (without competition) of plants along a gradient of nutrient stress. Their results showed distinct differences between the physiological and ecological responses of the five species examined. They also noted that the ecological response of most species varied with the species composition of the competitive background. This study underscored the importance of both distinquishing between the ecological and physiological responses of plants and providing a realistic environmental background if a more realistic ecological response is to be evaluated.

Ultraviolet radiation has been recognized as an environmental stress for over a century (Caldwell 1981). However, studies on its effects on plants have been conducted only within the past twenty years. These studies have largely focused on single plant physiological response to ultraviolet radiation stress. Very few studies on the ecological effects of ultraviolet radiation upon plant species interactions have been undertaken (Fox and Caldwell 1978, Bogenrieder and Klein 1982). A literature review on the effects of ultraviolet radiation on plants is provided by Caldwell (1981).

Although ultraviolet radiation comprises only a small portion of the total flux of solar radiation, it can have a disproportionately large effect on biological systems. Many higher terrestrial plants are functionally sensitive to ultraviolet-B radiation (280-320 nm) (Biggs et al. 1975). Ultraviolet-B radiation is absorbed by some cellular constituents, such as DNA and nucleic acids. These chromophores are often damaged by absorption of UV-B radiation under conditions of artificial irradiance (Harm 1979, Rothman and Setlow 1979). However, due primarily to absorption by stratospheric ozone, essentially no radiation shorter than 295 nm currently reaches the earth's surface. The shorter wavelength ultraviolet radiation that is transmitted comprises the solar UV-B (295-320 nm). Little direct evidence exists that indicates that current levels of solar UV-B irradiance have a substantial limiting effect upon plant growth and development. Becwar et al. (1982) found no change in the dry weight of wheat, potato and radish monocultures grown under UV-B exclusion relative to control plants under a high ambient UV-B flux (Colorado, 3000 m elevation). Only plant height changed significantly (increased) under solar UV-B exclusion. Bogenrieder and Klein (1982) provide some evidence that indicates that current levels of solar UV-B affect plant competition in an area of not particularly intense solar radiation (Freiburg, West Germany, 200 m altitude, 48^{o}N. latitude). Observations on the promotion of flowering in some alpine plants (Caldwell 1968) and the reduction of solar injury in some melon species (Lipton and O°Grady 1980) through exclusion of solar UV-B suggests some effect, but substantial evidence is still lacking.

Because of man°s release of chlorofluoromethanes (CFMs) and related compounds to the atmosphere, the stratospheric ozone layer may be reduced (NAS 1979). The CFMs provide a stable source of chlorine to the stratosphere, where it acts in the catalysis of ozone disassociation. Current atmospheric models (Green et al. 1980) predict that this ozone reduction will result in both an increase in the absolute flux of solar UV-B radiation and a slight spectral shift to include some shorter, more actinic wavelengths (Fig. 1). For a given flux of radiation, UV-B has a much more pronounced effect upon biological systems than the longer wavelength ultraviolet radiation (UV-A: 320-400 nm), which currently comprises most of the solar UV radiation flux (Fig. 2). Hence, the impact of the currently predicted 7-16% ozone reduction (NAS 1979, 1982) could be very significant in terms of increasing the biologically effective UV-B radiation flux and enhancing its importance as an environmental stress. This increase of UV-B radiation over a relatively short time frame (50-100 years) could lead to changes in competition within plant communities through differential tolerance by plant species.

The interaction of ultraviolet-B radiation stress and competitive stress has been examined by Fox and Caldwell (1978). Competition between plants sown in pots was examined under artificial

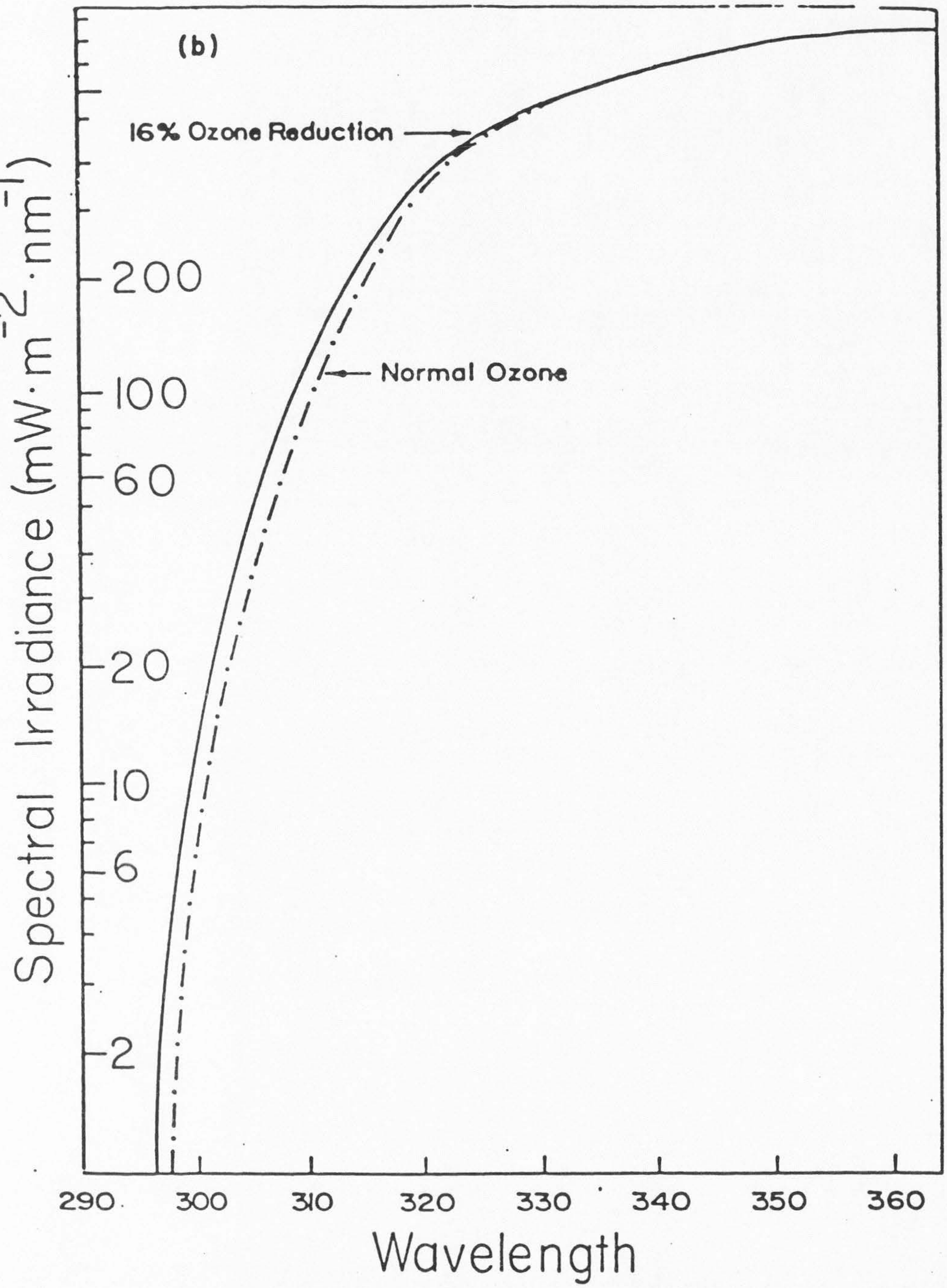


Figure 1. Theoretical values of solar UV spectral irradiance under current ozone levels and a 16% ozone reduction on August 20 at 1200 solar time (40° N. latitude and 1500 m elevation). These values are calculated by the model of Green et al. (1980).

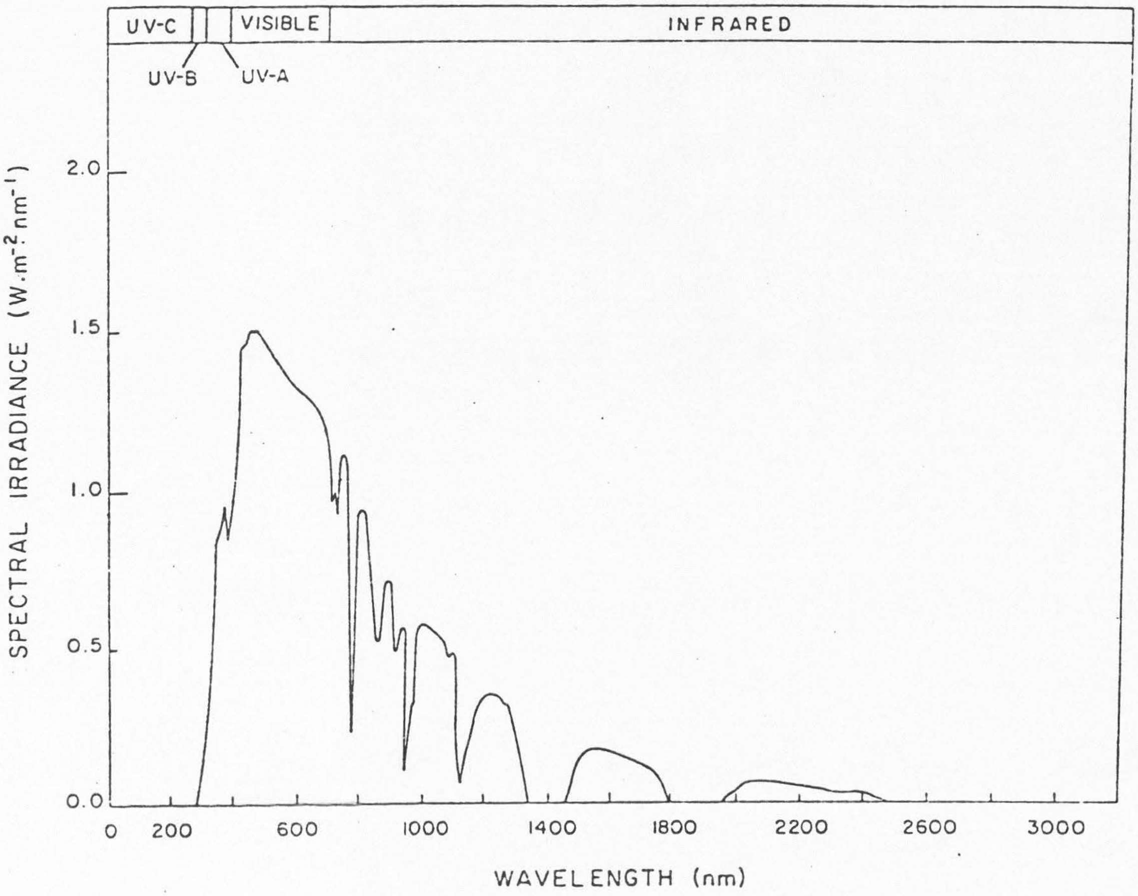


Figure 2. Solar spectral irradiance incident at the earth's surface.

enhancement of UV-B irradiance in the field. Their study involved three general types of associated competitors: agricultural crops and their weedy associates, montane forage species, and weeds from disturbed areas. The competitive interactions were examined using a modified deWit (1960) replacement series experiment. Some of the general findings from this experiment were:

1. The competitive balance of some species pairs shifted under enhanced UV-B radiation.

2. Some species pairs showed no shift in competitive balance under enhanced UV-B, but did exhibit a shift in the manner of competitive interaction (i.e. a change in average plant weight but not total species biomass).

3. In some species pairs the effect of enhanced UV-B radiation was greater under higher levels of interspecific competitive stress. However, the opposite was also true in some cases.

4. In most cases where enhanced UV-B radiation resulted in increased growth of one species, the growth of its competitor was depressed.

The implications of these results, in part, form the basis for the objectives and hypotheses proposed in this study. The first two results imply that an enhanced UV-B radiation regime can alter the competitive situation of at least some of the competing species pairs. The third result suggests that the level of interspecific competitive stress does affect the manifestation of UV-B radiation stress, but the nature and direction of that relationship is unclear. The last result indicates that some species can be indirectly benefited by an enhanced UV-B radiation regime through an alteration of the competitive situation (probably through competitive release). The results of these experiments, however, must be treated with caution as to their ecological significance because of the factors associated with the experimental design (i.e. very large UV-B supplement, high plant densities, a shifted growing season, lack of natural water stress, and pot-grown plants). Nevertheless, the results do provide preliminary insights into the nature of the interaction between UV-B radiation and plant competition.

In agricultural situations, interspecific competition can be an important factor in decreasing harvest yields (Brown 1955, McWhorter and Patterson 1980). Therefore, an alteration of the competitive balance between agricultural species and their associated weeds could have serious implications in terms of agricultural yields. Because of the projected increase in UV-B radiation flux (NAS 1979, 1982), the understanding of its possible effects upon plant competitive balance in agricultural situations is very important. Fox and Caldwell (1978) have shown a marked shift in competitive balance (significant changes in species biomass production) between alfalfa (*Medicago sativa*) and redroot pigweed (*Amaranthus retroflexus*) under an enhanced UV-B radiation regime. Significant changes in the yields of any such major crop species, as a result of shifts in competitive situations, could have serious consequences for an already problematic world food supply.

Plant competition is a conflict for resources which necessarily has both spatial and temporal components. Competition occurs when two or more neighboring individuals attempt to acquire the same limited resource at the same time. This study examined relative changes in shoot biomass, which suggests the existence of plant interference (Harper 1977). Although competition is the most likely form of interference, the lack of evidence for a resource limitation leaves open the possibility of other forms of interference (e.g. allelopathic interactions) being responsible for the observed results. Plant competition is manifested upon an individual plant through an increase in environmental stress, rather than having a direct effect *per se*. For example, the actual effect of competition for water by individual plants will be increased water stress (and perhaps nutrient stress) for those individuals. Since plants probably often compete for more than one resource over a short period of time, competition may induce complex changes in the entire suite of stresses that act upon the individual plants.

Analysis of plant competition can be accomplished through replacement series experiments described by deWit (1960). In these experiments, the competitors are grown together in varying proportions, and their production in these mixtures is compared to their production in monoculture. This allows the calculation of k , the relative crowding coefficient, which is a relative measure of the competitive ability of one species when it is grown in mixture with a second species. The relative crowding coefficient (k_{12}) can be calculated by :

$$k_{12} = \frac{O_1 \cdot M_2 \cdot Z_2}{O_2 \cdot M_1 \cdot Z_1} \qquad (1)$$

where M is the yield of the particular species (1 or 2) in monoculture, O is the yield of the particular species in mixture, and Z is the number of plants of that particular species in the mixture. Calculated in this manner, when k_{12} is greater than 1.0, the first species has a competitive advantage and when k_{12} is less than 1.0, the second species has a competitive advantage. When k_{12} equals 1.0, neither species has a competitive advantage. The monoculture and mixture yields can be measured using any parameter that gives an appropriate reflection of species' competitive ability (e.g. biomass, seed production). Calculated in this manner (Harper 1977), k_{12} is an estimate of the relative crowding coefficient introduced by deWit (1960). The major assumption involved with the calculation of this crowding coefficient is that the two species tend to competitively exclude each other directly.

The relative yield total (RYT) of a mixture is another parameter that can be calculated to characterize a competitive situation (deWit 1960, Harper 1977):

$$RYT = \frac{O_1}{M_1} + \frac{O_2}{M_2} \quad . \qquad (2)$$

The value of RYT can be used to infer the amount to which the two species are making demands on the same environmental resources or, in other words, their degree of interspecific competitive overlap. Values of RYT of about 1.0 indicate a high degree of competitive overlap, while values of RYT greater than 1.0 indicate a decreased competitive overlap. A decrease in the degree of competitive overlap also implies a more complete use of the available resources by the species. A value of RYT less than 1.0 implies a mutual antagonism (Harper 1977).

Recently, deWit replacement series analysis has been criticized as a means of evaluating the nature of a competitive situation because of its density independent qualities. Inouye and Schaffer (1981) pointed out that by varying overall experimental densities, replacement series analysis can yield different competitive results. Thus, they conclude that overall density, as well as frequency should be varied for a correct analysis. Although this is a valid criticism, the deWit analysis was primarily developed for use in agricultural situations, where overall densities are often relatively constrained.

Wheat (Triticum aestivum L.), the most important world agricultural crop in terms of biomass production (Martin et al. 1976), was chosen as the major crop species for this study. A limited amount of data on the response of wheat to supplemental UV-B radiation has been gathered by Biggs and Kossuth (1978). In general, they found that wheat was relatively insensitive to supplemental UV-B when compared to most other species tested. Although their data may give a useful relative measure of UV-B sensitivity, the growth of plants in pots within a growth chamber and the exclusion of natural competitors limits the ecological and predictive significance of any absolute measures of UV-B sensitivity.

The two competitors chosen for use in these experiments were wild oat (*Avena fatua* L.) and jointed goatgrass (*Aegilops cylindrica* Host). Wild oat is a common weed in wheat fields and a substantial amount of work has been devoted to examining its effect on wheat yields (Tingey 1965, Henson and Jordan 1982). Jointed goatgrass is also a common weed, occuring more often along field margins than in the field itself. Both species have phenological patterns similar to wheat, thus simplifying radiation supplementation and growth analysis. Neither of these species has been previously examined for UV-B response and sensitivity.

OBJECTIVES AND HYPOTHESES

The objectives and alternative hypotheses of this study, accompanied by a brief rationale for each, are outlined in this section.

Objective 1: To determine the effect of an increased ultraviolet-B radiation regime on the competitive balance and competitive interaction of wheat and some common competitors, wild oat and jointed goatgrass.

Hypothesis 1a: An enhanced ultraviolet-B radiation regime will alter the competitive balance of wheat and either competitor, wild oat or jointed goatgrass.

Rationale: Previous research (Biggs and Kossuth 1978) has indicated that plants exhibit a wide spectrum of sensitivities to UV-B radiation stress. Because of this differential sensitivity, the relative vigor of competing plant species may be altered, thus causing a change in the present competitive situation.

Hypothesis 1b: An enhanced ultraviolet-B radiation regime will not alter the total aboveground production of mixed species plots.

Rationale: Differential sensitivity to increased UV-B radiation should facilitate a growth increase by the less sensitive species in response to reduced competition from the more sensitive species, resulting in little net change in total mixture plot production.

Objective 2: To examine the effect of an increased UV-B radiation load on wheat, wild oat, and jointed goatgrass in monoculture.

Hypothesis 2: Increased UV-B radiation will result in a decrease in monoculture biomass production of each species.

Rationale: The current understanding of mechanisms of UV-B action upon plants suggests that UV-B radiation should usually be detrimental. Thus, UV-B enhancement should decrease the production of pure stands.

Objective 3: To examine the effect of an increased UV-B radiation stress on the pattern of reproductive allocation in wheat, wild oat, and jointed goatgrass.

Hypothesis 3: Increased UV-B radiation will alter the relative proportion of biomass allocated to reproduction in any of the three study species.

Rationale: The relationship between proportional allocation to reproduction in plants and various combinations of stresses present is not clear. Cultivated plant species have been shown (Harper 1977) to demonstrate little response, except in cases of extreme stress. This, however has been shown only in the case of a gradient of one stress. The response to a combination of stresses such as increased UV-B radiation and interspecific competition is uncertain. In addition, the plasticity of fractional reproductive allocation (in response to changes in the environment) may differ between cultivated species (wheat) and weedy species (wild oat and jointed goatgrass).

Objective 4: To examine the effect of different water stress regimes upon the interaction between plant competition and increased UV-B radiation.

Hypothesis 4: When water stress is reduced, the effect of UV-B stress will be more pronounced, especially at the end of the growing season when water stress is high.

Rationale: Water is the principal limiting factor in the growth of plants at the study site. Therefore, the effects of water stress (which increase as the growing season progresses) may mask the effects of UV-B stress upon plant competition.

METHODS

Radiation Methods

1981 Field Season

The level of ultraviolet-B radiation enhancement in this year of the study was chosen to represent UV-B conditions under a 16% reduction of the current ozone layer (low UV-B enhancement). This level of ozone reduction is slightly higher than the most recent prediction of ozone reduction (7-10%) by the National Academy of Sciences (1982) for equilibrium conditions within the next century. The calculation of the UV-B supplementation level for this study used the model of Green et al. (1980) for predicting incident ultraviolet-B radiation under certain atmospheric conditions (ozone concentration, solar angle, elevation above sea level, aerosol optical thickness, and ground surface albedo). This model was used to predict incident UV-B levels under current atmospheric conditions and conditions of a 16% reduction of the ozone layer. These results were weighted with the generalized plant action spectrum (Caldwell 1971) to obtain the "biologically effective" UV-B (UV-B_{BE}) fluxes, the difference of which is the amount of UV-B_{BE} supplement required in the field to realistically simulate a 16% ozone depletion under those atmospheric conditions. The ratio of UV-B_{BE} under 16% ozone reduction conditions to UV-B_{BE} under current conditions, or the radiation amplification factor (RAF), varied from 1.32 to 1.36 at solar noon throughout the growing season.

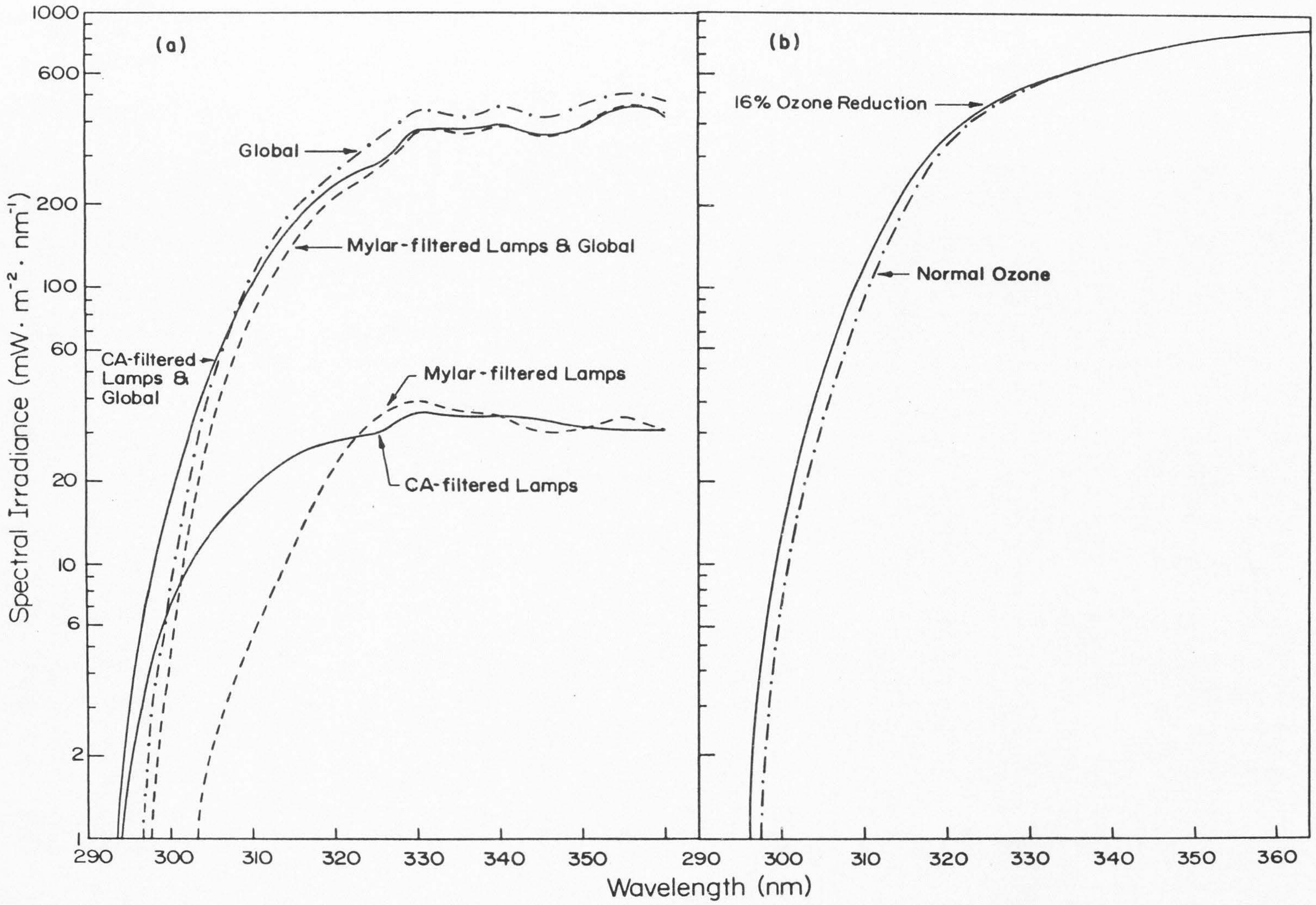
The ultraviolet-B radiation supplement was provided by lamp banks containing eight Westinghouse FS-40 sunlamps. These rectangular lamp banks measure 180 cm by 120 cm, with the bulbs spaced evenly along the 180 cm axis. The lamp banks are adjustable in height to allow a constant distance between the lamps and the plant canopy throughout the growing season (40 cm) and hinged to allow easy access to the plants for measurements. Plastic film filters were used to provide treatment (cellulose acetate, 5 mil) and control (mylar-D, 5 mil) irradiance conditions (Sisson and Caldwell 1975). All bulbs in each lamp bank were filtered with the same material, thus providing either treatment or control lamp banks. Cellulose acetate film was used for the UV-B enhancement treatment because its spectral cutoff value (lowest wavelength transmitted) approximates that of a predicted UV-B flux under a 16% ozone reduction. Mylar-D excludes all UV-B radiation and thus was used to provide control conditions. Control lamp banks were modulated at the same intensity as treatment lamp banks to control for the small amount of UV-A radiation emitted by the lamps.

Figure 3a shows the measured spectral irradiance from treatment and control lamp banks, with and without solar irradiance background. Figure 3b shows the results of the Green et al. (1980) model simulation for solar spectral irradiance under current and 16% reduced ozone conditions. Although the cutoff of the treatment lamp bank is similar to that of the enhanced model conditions, the lamps have a very different spectral emittance than the sun. Consequently, the spectral characteristics of the treatment lamp bank are different than the enhanced model prediction. Therefore, the UV-B radiation flux must be weighted with an appropriate biological action spectrum so lamp system output can be compared to solar irradiance.

The control of UV-B supplementation by the lamp banks was accomplished by specially developed modulation systems (Caldwell et al. 1983). The absolute level of UV-B supplementation was electronically adjusted at the start of the growing season for a constant lamp bank height of 40 cm above the average plant canopy. Once set, the modulation system monitored and adjusted the lamp output in accordance with changes in ambient UV-B flux and lamp/filter system output. Verification of the low UV-B enhancement (simulation of a 16% ozone reduction) under treatment lamp banks (Fig. 4) showed that the measured biologically effective supplement was within two percent of the desired supplement throughout the course of a day on August 17, 1981. In addition, the lamp frames were oriented perpendicular to the daily path of the sun. This caused the shadows cast by the lamp bank to move uniformly across the entire plot through the day.

The plastic film filters were changed every two weeks to prevent significant accumulation of dirt and dust on the filter material. The absolute level of $UV\text{-}B_{BE}$ radiation supplementation was also adjusted to compensate for the reduction in incident $UV\text{-}B_{BE}$ flux

Figure 3. (a) Spectral irradiance received at 40 cm under fluorescent sunlamp banks filtered with plastic film filters. The lamps for UV-B enhancement (filtered with cellulose acetate, CA, film) are adjusted to provide a UV-B supplement equivalent to a 16% ozone reduction under these conditions at 1200 solar time, on August 20, 1981, at 41° 45' N. latitude and 1460 m elevation. Spectral irradiance from these lamp banks is shown with and without background solar UV irradiance. The control banks (filtered with Mylar film) are adjusted to provide the same UV-A irradiance as is emitted by the CA-filtered lamps. Solar UV spectral irradiance above the lamp banks is also depicted. (b) Theoretical values of solar UV spectral irradiance for these conditions, as calculated by the Green et al. (1980) model, are shown for current ozone conditions and an ozone layer reduced by 16%.


(a)
(b)
Global
Mylar-filtered Lamps & Global
CA-filtered Lamps & Global
Mylar-filtered Lamps
CA-filtered Lamps
16% Ozone Reduction
Normal Ozone
Spectral Irradiance (mW · m⁻² · nm⁻¹)
Wavelength (nm)
1000
600
200
100
60
20
10
6
2
1
290
300
310
320
330
340
350
360

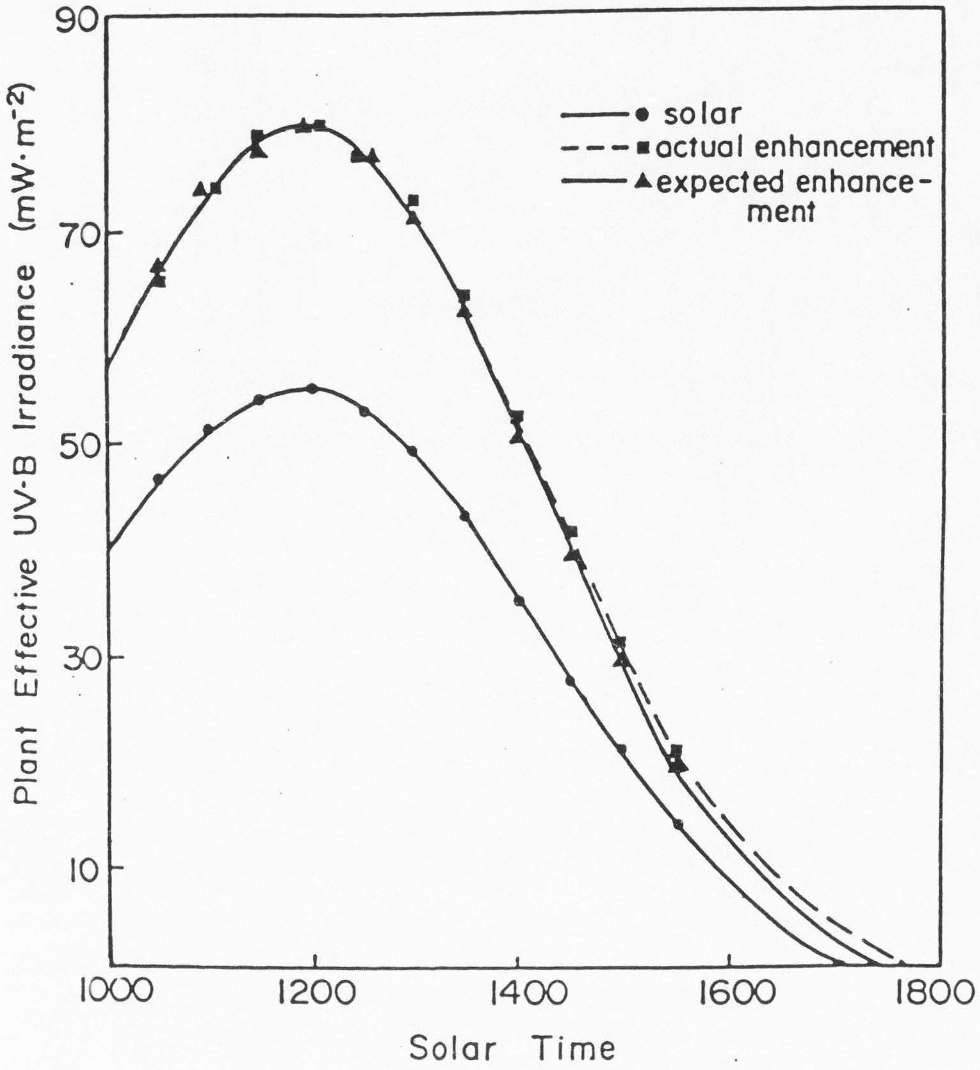


Figure 4. Results of spectral irradiance measurements of the UV-B radiation supplement provided by a treatment lamp bank compared with the theoretical desired supplement, as calculated by the model of Green et al. (1980). All values are expressed as integrated weighted irradiance (using the generalized plant action spectrum). The measurements were taken August 17, 1981.

caused by shading from the filters and the bulbs. The relative amount of UV-B_{BE} flux in both shaded regions was compared to that in the unshaded regions and calculations indicated that the total amount of shading reduced the incident UV-B_{BE} flux by ten percent. Thus, the UV-B_{BE} supplement was increased by ten percent over the amount determined in the previously discussed calculations to compensate for the shading effect. The effect of shading on UV-A flux is also evident in Figure 3a. The measurements for both treatment and control lamp banks are below those of the solar irradiance for the UV-A waveband, indicating that more solar UV-A is being shaded than compensated for by lamp output.

UV-B radiation levels were continuously monitored above and below the lamp banks with Robertson-Berger integrating sensors (Caldwell et al. 1983). Detailed dosimetery was performed with an Optronics model 742 spectroradiometer in conjunction with a Hewlett Packard HP-85 data acquisition system. This instrumentation system allowed direct computation of weighted (e.g. biologically effective) UV-B flux in the field and thus rapid adjustment and fine tuning of the modulation system when necessary. Photosynthetically active radiation (PAR: 400-700 nm) was continuously monitored under one of the lamp banks at average plant canopy height with a quantum sensor (LiCor Co.). Shading of PAR due to the lamp banks was about twenty five percent on a daily integrated basis, although daily peak PAR flux was not substantially reduced.

Measurements were taken in the field with a handheld Robertson-Berger meter to determine the usable "uniform radiation field" under the lamp bank. This field is defined as the area under the lamp bank that receives at least ninety percent of the peak irradiance from the lamps at the center of the bank. The uniform radiation field at a distance of 40 cm from the lamps was determined to be 123 cm by 61 cm and all experiments were conducted within this area.

1982 Field Season

In the second year of the study two levels of ozone reduction, sixteen (low UV-B enhancement) and forty percent (high UV-B enhancement), were simulated. For each pair of treatment lamp banks (one 16% and one 40% ozone reduction simulation) one control lamp bank, modulated at an intermediate intensity (28% ozone reduction), was used. Although this did not exactly control for lamp output of UV-A, the lamp output of UV-A is probably negligible relative to the ambient levels of UV-A radiation present. Three experimental groups, each consisting of two treatment and one control lamp bank, were set up for harvesting at three different times during the field season. Two additional pairs of treatment and control lamp banks, each simulating a sixteen percent ozone reduction and control, were used to test the effect of water stress. Water stress was reduced in these plots through daily supplemental drip irrigation. Volumetric soil water content was monitored by the neutron probe technique for watered and unwatered plots (Fig. 5). The watered treatment plots simulated a 16% ozone reduction.

The shading of $UV\text{-}B_{BE}$ was reevaluated at the start of the 1982 field season and was determined to be about twenty percent, about twice that assumed for the first field season. During the 1982 field season, the usable uniform radiation field was increased to 150 cm by 61 cm by proportionately boosting the output of the outer lamps in the lamp bank (Caldwell et al. 1983).

Competition Materials and Methods

Seed for the wheat cultivar, Bannock (a hard, red spring wheat), used in the experiments was obtained each year from the Utah State University Blue Creek experimental farm. The wild oat seed was obtained locally from a fallow small grain field and the jointed goatgrass seed was collected from a local roadside disturbed area (1600 m elevation).

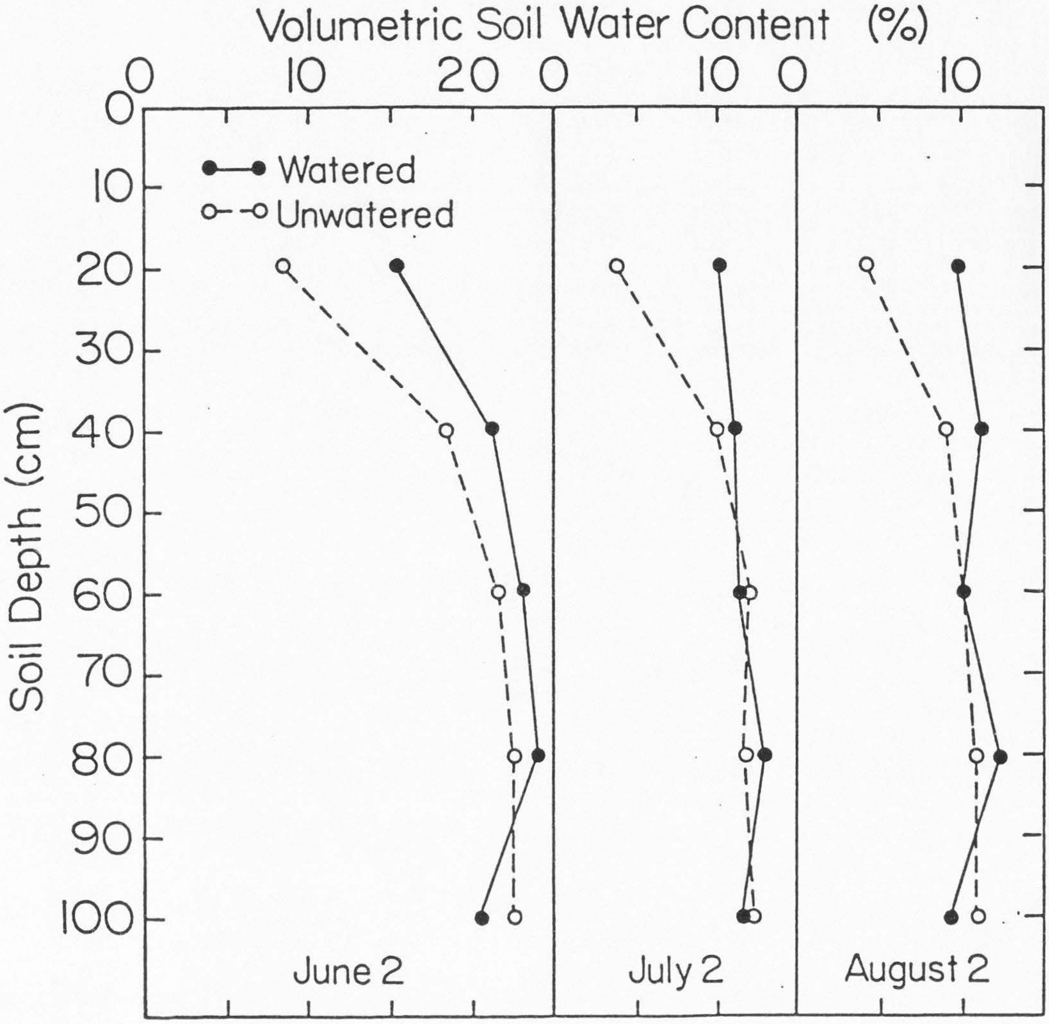


Figure 5. Volumetric soil water content for watered and unwatered plots from 20 - 100 cm during the 1982 growing season. Values were obtained by the neutron probe technique.

1981 Field Season

The effect of enhanced ultraviolet-B radiation stress on the competitive balance and interaction of wheat and either weed (wild oat or jointed goatgrass) was examined using a deWit (1960) replacement series design. A constant density of 62 seeds per square meter was sown in each experimental unit, but the relative frequencies of the competitors were varied. Three replicates of each of the five frequency combinations were used:

Seeding Proportion	Seeds Sown
1.0 : 0.0	56 wheat seeds : 0 weed seeds
0.8 : 0.2	44 wheat seeds : 12 weed seeds
0.5: 0.5	28 wheat seeds : 28 weed seeds
0.2 : 0.8	12 wheat seeds : 44 weed seeds
0.0 : 1.0	0 wheat seeds : 56 weed seeds

The seeds were sown in an evenly spaced grid within each experimental unit. Widely different germination of all species in the experimental units resulted in a large variation in both species relative frequency and overall plot density.

The experiments were conducted at the Green Canyon Ecology Center located north of the Utah State University campus in Logan, Utah. Each field plot under a lamp bank measured 123 cm by 183 cm and all contained the same homogenous soil to a depth of 90 cm. In the fall of

1980 each plot was excavated to a depth of 120 cm, the lower 30 cm homogenized and replaced, and the top 90 cm filled with uniform silty loam soil brought in from a local source. Studies in the Plant Science Department at Utah State University indicate that most of the water and nutrient uptake of spring wheat occurs in the upper 115 cm of the soil profile. Each plot was bordered by cedar boards to prevent overland water flow and erosion problems. The uniform radiation field within each plot was divided into eight 30 cm by 30 cm experimental units. An entire set of eight experimental units was randomized within each major treatment (under each lamp bank). There were three treatment lamp banks and three control lamp banks, thus providing three replicates of each experimental unit within each treatment. To reduce border effects a 5 cm unsampled border was left on each replicate plot of 30 cm by 30 cm. The area surrounding the uniform radiation field in the plots was also sown with wheat as a buffer against the outside environment.

Planting took place on June 19, 1981. Overall plot density and species composition were assessed one to two weeks following emergence (early July). At that time, three individual plants from each species in each experimental unit replicate were tagged as "model plants". Model plants were chosen as average or representative plants of each species in each experimental unit. Nondestructive sampling of these model plants was accomplished three times during the growing season: July 13, July 27, and August 10, 1981. A final destructive sampling was conducted on August 24, 1981. The nondestructive parameters measured included plant height, number of leaves, number of tillers, length of the longest leaf, and number of seedheads per plant. In addition, at each of these sampling dates biomass was determined for plants of each species in a separate "sacrifice" plot. These data were used to determine species specific biomass regressions for each date. The plants in the sacrifice plot were planted in monocultures and subjected to an unmodulated treatment irradiance level (low UV-B enhancement). Multiple regression analysis of the sacrifice data, using shoot biomass as the dependent variable and the nondestructive parameters as the dependent variables, allowed conversion of the nondestructive data from model plants to biomass (Table 1). These shoot biomass estimates were used for analysis of competition (e.g. calculation of crowding coefficients) during the season. Throughout the study the relative crowding coefficients were calculated for wheat (species 1) with respect to the weed (species 2).

All of the experimental units were harvested on August 24. The model plants were removed individually for separate analysis of seed production (numbers and weight) and biomass. The remainder of the plants in each experimental unit were removed by species for group analysis of reproductive and vegetative biomass. Reproductive production was defined as the seeds, seedheads, and the portion of the culm above the flag leaf. This is a convenient designation of reproductive production, and it is recognized that it does not include other portions of the plant that may be present only when the plant

Table 1. Biomass regression relationships for individuals of each species from sacrifice plants.

Sample Date	Taxon	Regression Equation*	R^2
July 13	Wheat	$Y = -0.0679 + 0.0021\ X_1 + 0.0073\ X_2 + 0.0173\ X_3$	.82
	Wild Oat	$Y = -0.0442 - 0.0247\ X_1 + 0.0032\ X_2 + 0.0241\ X_3$	.81
July 27	Wheat	$Y = -0.9610 + 0.1070\ X_1 + 0.0313\ X_2 + 0.0267\ X_3 + 0.0006\ X_4$	.92
	Wild Oat	$Y = -0.8800 - 0.0367\ X_1 + 0.0260\ X_2 + 0.0563\ X_3 + 0.0159\ X_4$	.94
August 10	Wheat	$Y = -1.8200 + 0.4920\ X_1 + 0.0493\ X_2 - 0.0908\ X_3 + 0.294\ X_4$	.90
	Wild Oat	$Y = -0.0151 + 0.0043\ X_1 + 0.0255\ X_2 + 0.0023\ X_3 + 0.187\ X_4$	.95

Sample Date	Parameters				
	Y	X_1	X_2	X_3	X_4
July 13	Biomass (g)	# Tillers	Plant Ht. (cm)	# Leaves	------
July 27	Biomass (g)	# Tillers	Plant Ht. (cm)	# Leaves	Length longest leaf
August 10	Biomass (g)	# Tillers	Plant Ht. (cm)1	# Leaves	# Seedheads

*All of the regressions were significant at P<.05.

achieves the reproductive stage (i.e. elongated sheaths, lower culm portions, etc.). The jointed goatgrass plants did not reach reproductive status due to the late planting date, and thus, no data on reproductive effort for wheat/jointed goatgrass plots or jointed goatgrass monocultures are available. The data on biomass throughout the season allowed calculation of crowding coefficents and relative yield totals (deWit 1960). All references to biomass in these experiments include only aboveground plant production, as no belowground data were collected. Seed production data were used to evaluate competitive ability in terms of reproductive effort through a similar competition analysis as that used for biomass.

The statistical model used for the evaluation of the treatment (low UV-B enhancement) effect was:

$$Y = u + T_i + b_1X_1 + b_2X_2 + e_{ij} \qquad (3)$$

where Y is the relative crowding coefficient, relative yield total, total mixture biomass production, or fractional reproductive effort; u is the mean; T_i is the treatment effect; b_1X_1 is the effect of experimental unit density; b_2X_2 is the effect of experimental unit species proportion; and e_{ij} is the error term. To detect a treatment effect, the model was verified first to test whether it explained a significant amount of the variability (alpha = .05 level) in the Y term. The treatment effect was then tested in the multiple regression model (ANOVA).

The effect of an enhanced UV-B radiation regime on the monoculture production of wheat, wild oat, and jointed goatgrass was also examined. Four densities of wheat (31, 62, 93, and 124 plants/m^2) and two densities of each weed (62 and 124 plants/m^2) were used in the original planting. Once again, varying germination resulted in a spectrum of monoculture densities for each species, necessitating the use of a regression model for the analysis. The physical design and replication were identical to that used in the interspecific competition experiment described above. The statistical design was also the same except for the abscence of a covariate term (X_2) for experimental unit species proportion. The independent variables (Y) analyzed in this case were biomass production and fractional reproductive effort. The sampling technique and parameters measured were also the same as those described in the interspecific competition experiment. The monoculture data of jointed goatgrass (62 plants/m^2) were used to provide the interspecific competition experiments with data for the jointed goatgrass monocultures.

1982 Field Season

In the second field season, the experiments were confined to a more detailed examination of the effects of enhanced UV-B radiation on interspecific competition between wheat and wild oat. A simplified deWit (1960) replacement series design was used with the overall density the same as that used in 1981. The frequencies of plants used were:

Seeding Proportion	No. of Plants Used
1.0 : 0.0	48 Wheat : 0 Wild Oat
0.5 : 0.5	24 Wheat : 24 Wild Oat
0.0 : 1.0	0 Wheat : 48 Wild Oat

Planting took place on May 12, 1982. In this case, the plots were overplanted and thinned down (in a grid pattern) to the correct overall density and relative frequencies indicated above. This eliminated the need for a multiple regression analysis, and an analysis of variance was used to analyze the resulting independent variables (relative crowding coefficient, relative yield total, total mixture plot biomass, and fractional reproductive effort, and monoculture biomass production). Differences among means were statistically tested with the Least Significant Difference (LSD) test (Zar 1974).

Each treatment plot contained four replicates of the three seeding proportions, or twelve experimental units. Each experimental unit measured 25 by 30 cm. At three times during the growing season (June 21, July 8, and August 2) an experimental set of three plots was harvested. One control plot and two treatment plots, simulating a UV-B flux under a sixteen and a forty percent ozone reduction, comprised each experimental set. The plants were harvested by species for each experimental unit and both vegetative and reproductive aboveground biomass were determined. These values were used to calculate the same parameters as in the 1981 field season. In the water stress interaction experiment, one treatment and one control plot were harvested June 21 and the remaining pair of plots was harvested August 2. The data taken were the same as that described above.

RESULTS

Monoculture Production

The multiple regression model for wheat monoculture production in 1981 indicated that low UV-B enhancement did not affect total biomass production at any time during the growing season (Table 2). No significant effect of UV-B radiation was detected on monoculture production for wild oat and jointed goatgrass as well (Table 2).

In 1982, a significant depression in wheat monoculture production occurred under low UV-B enhancement on June 21 and July 8 (Fig. 6). However, this depression was not evident in the final harvest on August 2. Wild oat monocultures showed no significant declines in production due to enhanced UV-B radiation. Data for the low UV-B enhancement on July 8 were not included for the wild oat monoculture plots because they were markedly chlorotic. An unexpected increase in production of wild oat monocultures occurred under high UV-B enhancement at the end of the 1982 growing season.

Competitive Interactions

The biomass relative crowding coefficients for the 1981 field season are presented in Table 3. The overall regression model

Table 2. Analysis of biomass production in monoculture of the three study species during the 1981 growing season.

Taxon	Model Portion	July 13	July 27	August 10	August 24
Wheat	Overall Model	SIG	SIG	SIG	SIG
	Treatment Effect*	NS	NS	NS	NS
Wild Oat	Overall Model	SIG	NS	NS	NS
	Treatment Effect*	NS	-	-	-
Jointed Goatgrass	Overall Model	SIG	SIG	NS	NS
	Treatment Effect*	NS	NS	-	-

SIG = Significant at $P < .05$.

NS = Nonsignificant.

*Low UV-B enhancement.

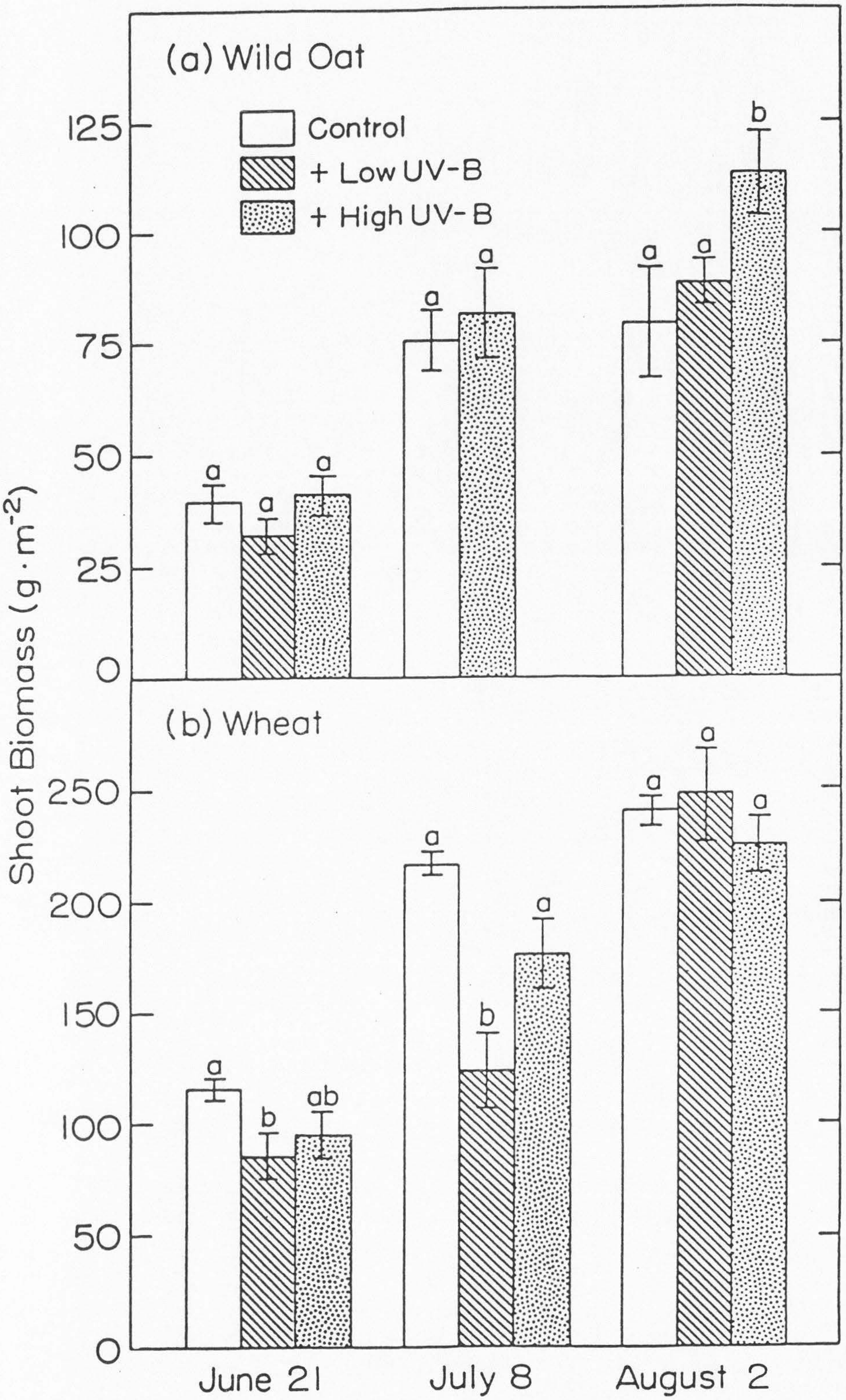


Figure 6. Shoot biomass production for wild oat (a) and wheat (b) in monoculture during the 1982 growing season. Each bar is the mean of four observations ($\pm$ 1 SE). Different letters indicate significant ($p < .05$) differences at each date by ANOVA.

was significant for three of four cases in the wheat/wild oat mixtures (where k_{12} is based upon total aboveground biomass production). In all three of those cases, the average treatment (+ low UV-B) crowding coefficient (n = 9) was significantly lower than the control crowding coefficient. This suggests that the competitive ability of wheat, relative to wild oat, was reduced by enhanced UV-B radiation throughout the growing season. This was also evident in the replacement series diagrams (Fig. 7) for the wheat/wild oat interaction. In the control replacement series diagrams the wheat curves were distinctly convex, whereas the wild oat curves were notably concave. This indicated a distinct competitive advantage for wheat under control conditions. However, this pattern was not exhibited in the treatment curves, where the curves of the species were similar for each date. This suggested a nearly equal competitive situation, which is corroborated by the treatment relative crowding coefficients being nearly equal to 1.0 (Table 3). The relative crowding coefficient based upon reproductive biomass production for wheat/wild oat mixtures did not exhibit any significant effect due to UV-B enhancement. Even though the means for the reproductive production data were quite different, the large variability precluded any statistically significant differences.

The total biomass relative crowding coefficients for wheat/jointed goatgrass mixtures in 1981 exhibited a significant increase under treatment UV-B irradiance for two sampling dates (Table 3). Therefore, for these two dates the competitive ability of wheat,

Table 3. Relative crowding coefficients (k_{12}) and relative yield totals (RYT) based upon total shoot biomass and reproductive biomass during the 1981 growing season.

		July 13	July 27	August 10	August 24
Wheat/Wild Oat k_{12} Shoot Biomass	Model	SIG	SIG	NS	SIG
	+ Low UV-B	1.05	0.99	-	1.22
	Control	1.52*	1.64*	-	1.52*
Wheat/Wild Oat k_{12} Repro. Biomass	Model				SIG
	+ Low UV-B				2.67
	Control				1.92
Wheat/J.G.Grass k_{12} Shoot Biomass	Model	NS	SIG	SIG	NS
	+ Low UV-B	-	1.35	1.57	-
	Control	-	0.54*	0.48*	-
Wheat/Wild Oat RYT Shoot Biomass	Model	SIG	SIG	NS	NS
	+ Low UV-B	2.12	2.88	-	-
	Control	1.94	1.95*	-	-
Wheat/J.G.Grass RYT Shoot Biomass	Model	NS	NS	NS	NS
	+ Low UV-B	-	-	-	-
	Control	-	-	-	-

SIG = Significant at $P<.05$.

NS = Nonsignificant.

*Significant ($P<.05$) effect of low UV-B enhancement. The sample size was nine observations in all cases.

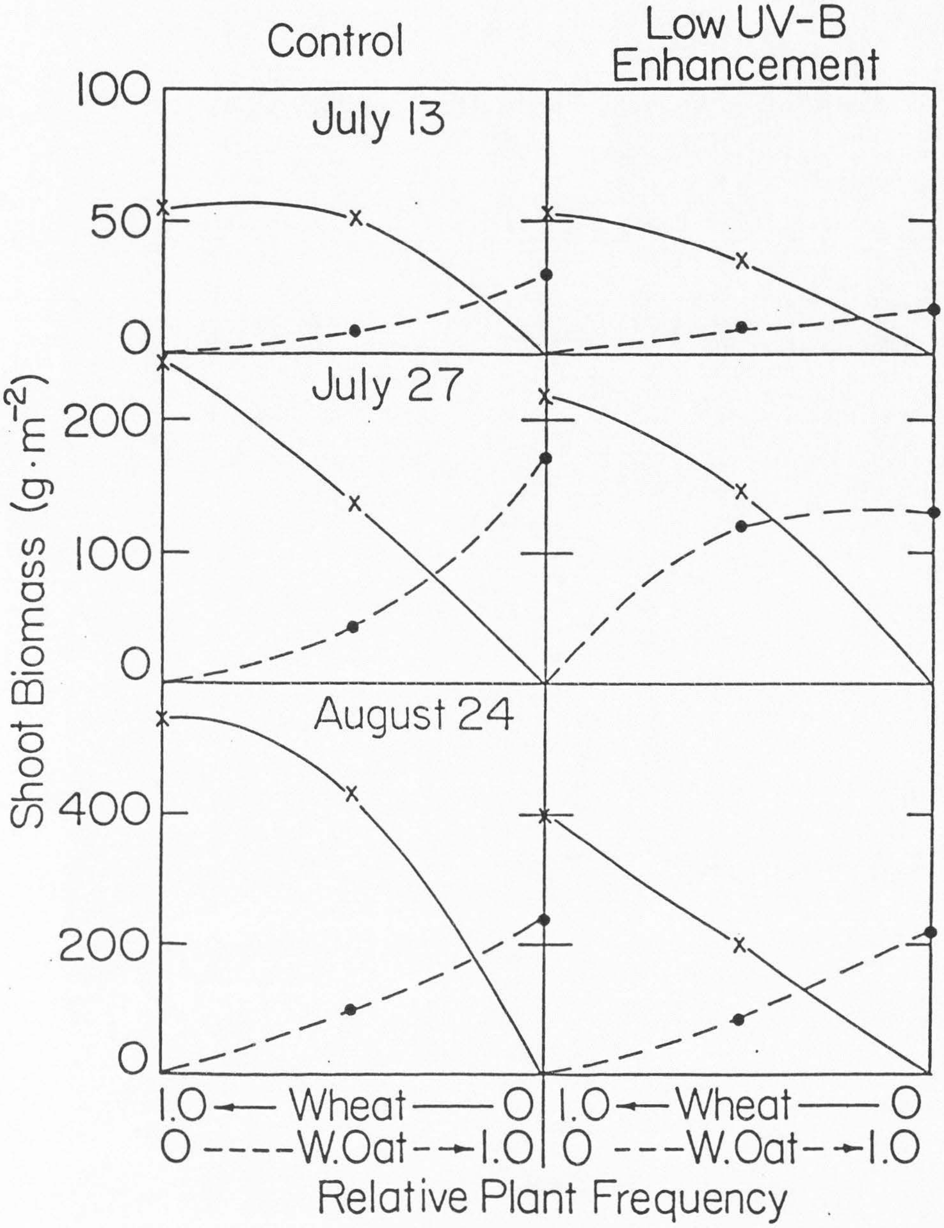


Figure 7. Replacement series diagrams of shoot biomass for wheat/wild oat competition during the 1981 growing season. Each point is the mean of nine observations.

relative to jointed goatgrass, was enhanced under increased UV-B irradiance. The competitive situation changed completely, from the control situation where jointed goatgrass was the dominant competitor ($k_{12}<1.0$) to the treatment situation, where wheat was the dominant competitor ($k_{12}> 1.0$). These shifts in competitive interactions were also evident in the replacement series diagrams for August 10 (Fig. 8). The pronounced convexity of the wheat curve in the treatment group indicated that wheat achieved competitive dominance under enhanced UV-B conditions.

The total biomass relative crowding coefficients for 1982 increased with increasing UV-B irradiance for wheat/wild oat mixtures during the entire growing season (Table 4). However, this increase in relative crowding coefficients was statistically significant only at the high levels of UV-B enhancement on June 21 and August 2. This suggested that the competitive ability of wheat relative to wild oat increased with increasing UV-B enhancement. This is contrary to the 1981 results for the wheat/wild oat mixtures. The replacement series diagrams for 1982 (Fig. 9) reflected these results, with increased convexity in the wheat curve and concavity in the wild oat curve with increasing UV-B enhancement.

The relative crowding coefficients based upon reproductive biomass for 1982 (Table 4) increased with increasing UV-B enhancement. Once again only the high UV-B enhanced treatment was significantly

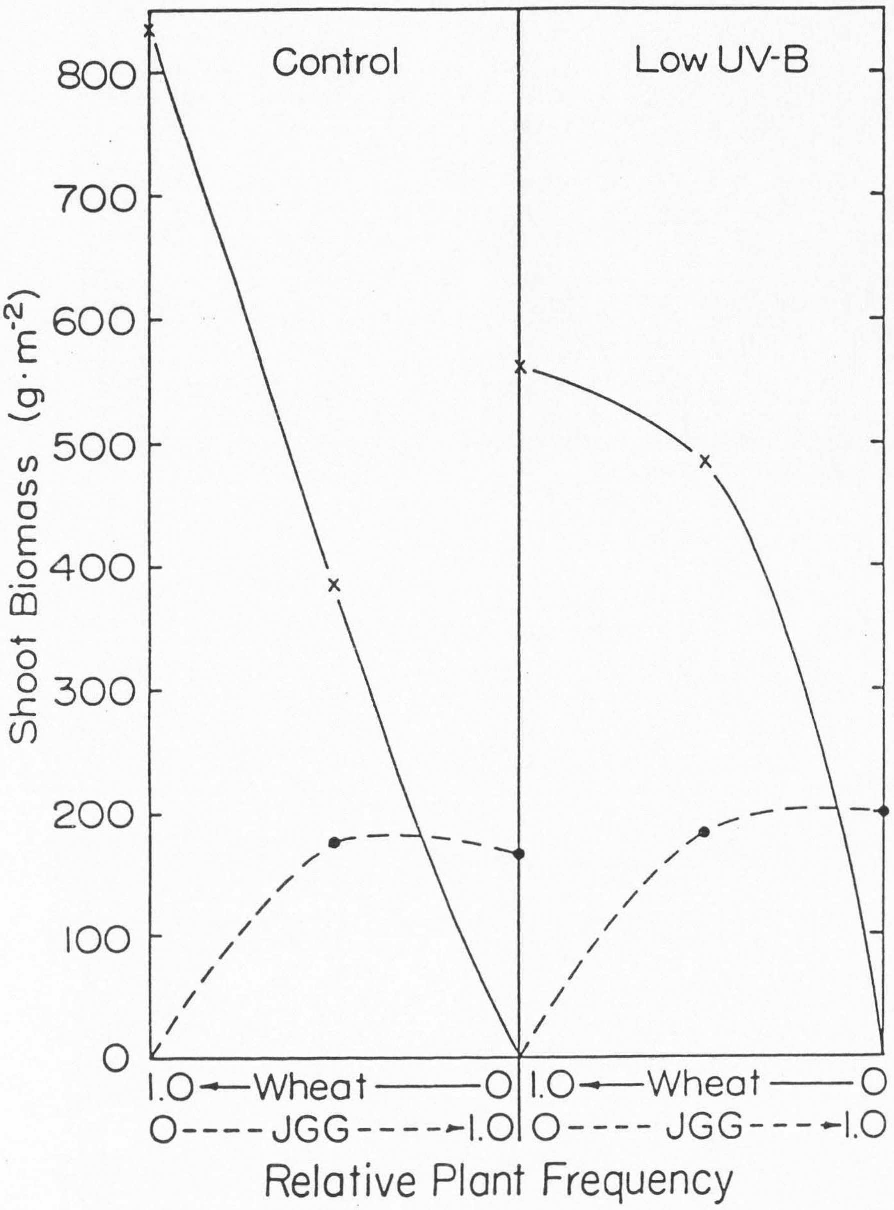


Figure 8. Replacement series diagrams of shoot biomass for wheat/jointed goatgrass competition on August 10, 1981. Each point is the mean of nine observations.

Table 4. Relative crowding coefficients (k_{12}) and relative yield totals (RYT) based upon total shoot biomass and reproductive biomass during the 1982 growing season.

Competition Parameter	UV-B Treatment	June 21 Shoot Biomass*	July 8 Shoot Biomass*	August 2 Shoot Biomass*	August 2 Repr. Biomass*
Relative Crowding Coefficient (k_{12})	Control	0.90^{a}	1.20^{bc}	1.08^{abc}	1.00^{a}
	Low Enhancement	1.10^{b}	1.30^{bc}	1.28^{bc}	1.18^{abc}
	High Enhancement	1.29^{c}	1.83^{cd}	1.69^{d}	1.41^{d}
Relative Yield Total (RYT)	Control	0.95^{a}	0.95^{a}	1.01^{a}	-
	Low Enhancement	1.12^{a}	0.99^{a}	0.94^{a}	-
	High Enhancement	0.99^{a}	1.09^{a}	0.98^{a}	-

*Different letters indicate significant ($P<.05$) differences within a column for each competition parameter. Each value is the mean of four observations.

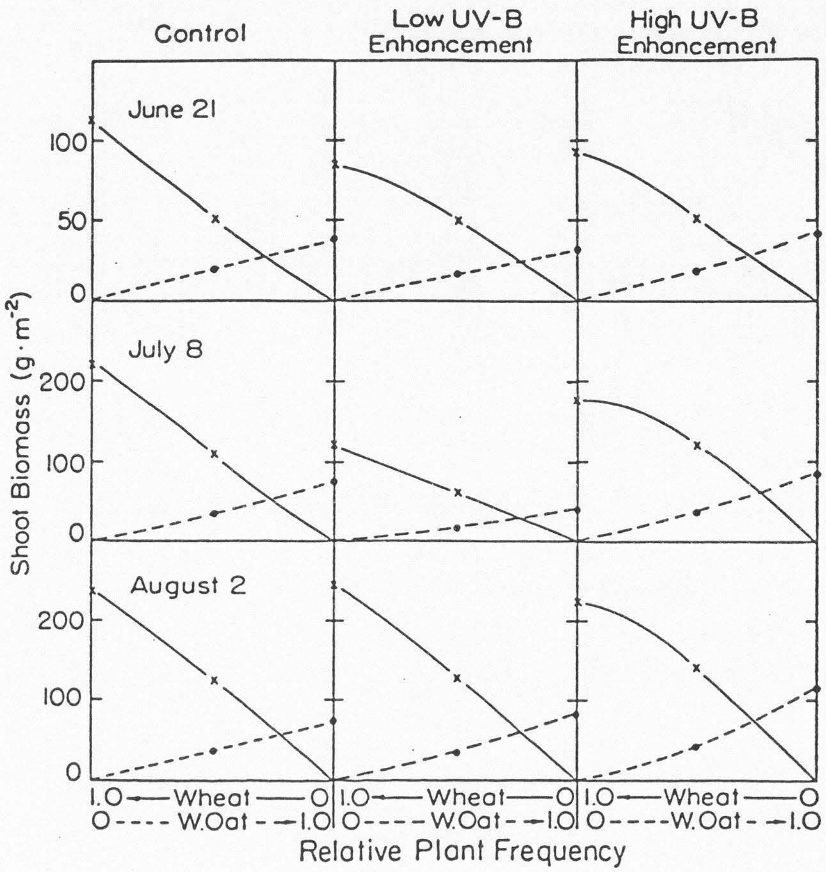


Figure 9. Replacement series diagrams of shoot biomass for wheat/wild oat competition during the 1982 growing season. Each point is the mean of four observations.

different from the control. Thus, in 1982 increased UV-B irradiance resulted in an increase in the competitive ability of wheat relative to wild oat in terms of both total biomass production (at any time during the growing season) and reproductive effort.

The total biomass production of mixture plots was not affected by UV-B enhancement in both 1981 (Table 5) and 1982 (Fig. 10). The data for the low UV-B enhancement on July 8 were not included because of the distinct chlorosis of that plot. Thus, although changes in competitive interactions occurred, the total productivity of these mixture plots was not altered.

The relative yield total in 1981 for the wheat/wild oat mixtures at the second sampling period was significantly higher under enhanced UV-B irradiance (Table 3). Although the same trend was evident on the first sampling date, it was not statistically significant. This suggested a decreasing competitive overlap under enhanced UV-B conditions for the wheat/wild oat mixtures. The regression model for the relative yield totals of wheat/jointed goatgrass mixtures was not significant at any sampling date (Table 3). Consequently, no data on the effect of UV-B enhancement are available. The 1982 relative yield totals for wheat/wild oat mixtures (Table 4) exhibited no distinct trends and were not statistically different on any date. As a result, in 1982 UV-B enhancement apparently had no significant effect on the degree of competitive overlap in wheat/wild oat mixtures.

Table 5. Analysis of total shoot biomass production in mixtures during the 1981 growing season.

Taxon	Model Portion	July 13	July 27	August 10	August 24
Wheat/Wild Oat	Overall Model	SIG	SIG	SIG	NS
	Treatment Effect*	NS	NS	NS	-
Wheat/Jointed Goatgrass	Overall Model	SIG	NS	SIG	NS
	Treatment Effect*	NS	-	NS	-

SIG = Significant at $P < .05$.

NS = Nonsignificant.

*Low UV-B enhancement.

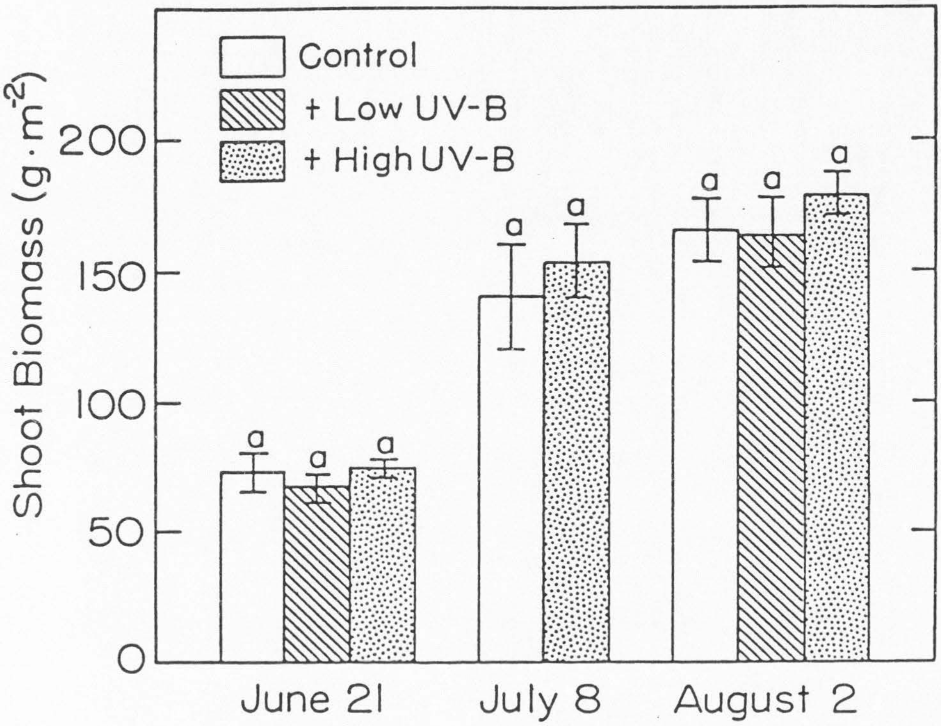


Figure 10. Total shoot biomass production of wheat/wild oat mixtures during the 1982 growing season. Each bar is the mean of four observations (± 1 SE). Different letters indicate significant ($p < .05$) differences at each date by ANOVA.

Reproductive Allocation

Fractional reproductive effort (reproductive biomass divided by total aboveground biomass) was difficult to analyze in 1981 due to the failure of the regression model to adequately explain the variability in fractional reproductive allocation in two out of four cases (Table 6). In the cases that were valid, the fractional reproductive allocation of wheat in monoculture and wild oat in mixture (with wheat) was not significantly affected by an enhanced UV-B irradiance.

The fractional reproductive effort of wheat in 1982 (Fig. 11) was also unaffected by enhanced UV-B irradiance in both monocultures and mixtures. This was also true for wild oat in monocultures (Fig. 11). However, the fractional reproductive allocation of wild oat in mixtures was significantly depressed by both high and low UV-B enhancement (Fig. 11).

Water Stress Reduction

Monoculture biomass production in the plots receiving supplemental irrigation was not affected by enhanced UV-B radiation for wild oat. However, wheat exhibited an unexpected increase in biomass under low UV-B enhancement on August 2 (Fig. 12). This is similar to

Table 6. Analysis of fractional reproductive effort for wheat and wild oat in monocultures and mixtures during the 1981 growing season.

Taxon	Model Portion	Monoculture	Mixture
Wheat	Overall Model	SIG	NS
	Treatment Effect*	NS	-
Wild Oat	Overall Model	NS	SIG
	Treatment Effect*	-	NS

SIG = Significant at P<.05.

NS = Nonsignificant.

*Low UV-B enhancement.

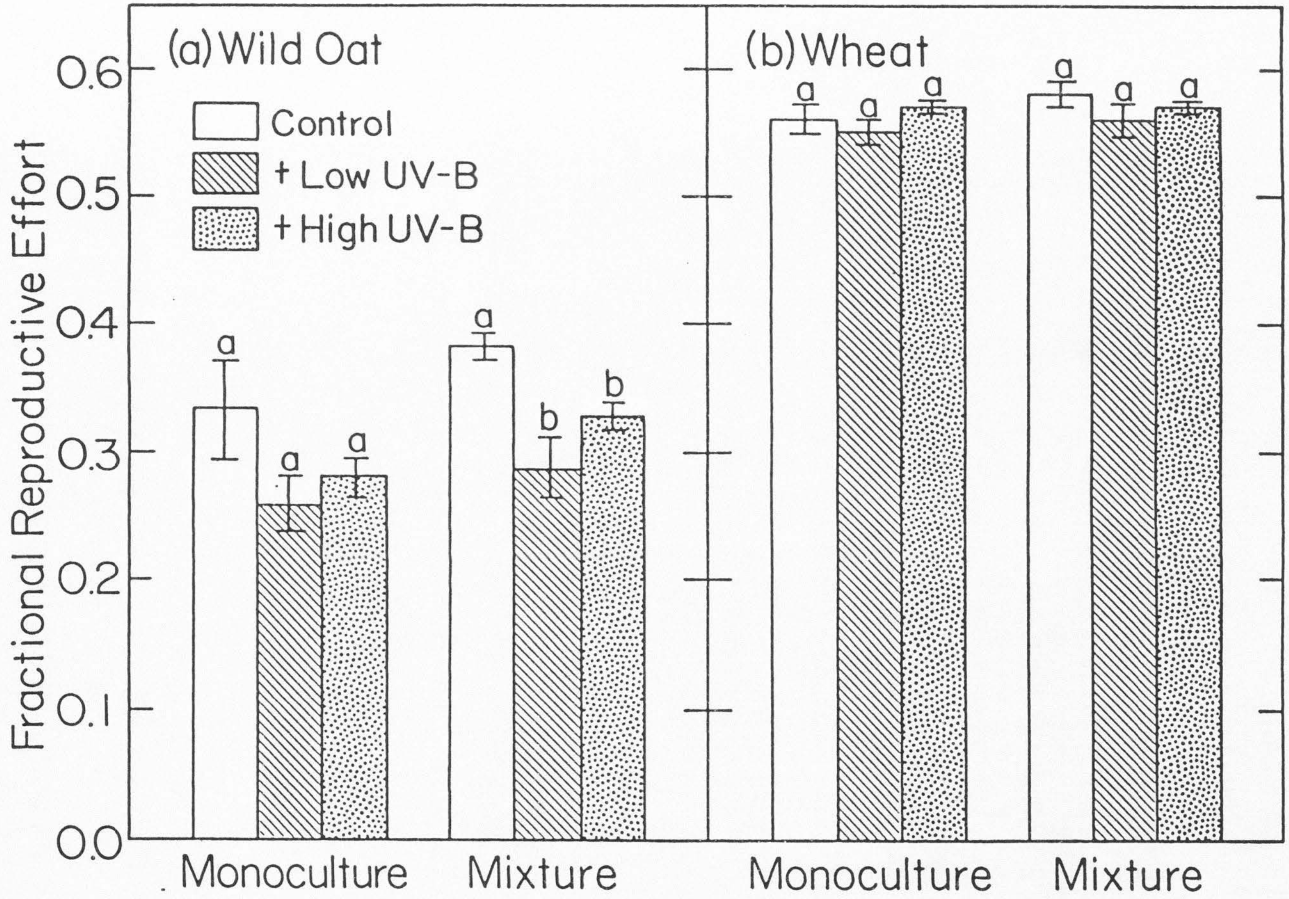


Figure 11. Fractional reproductive effort of wild oat (a) and wheat (b) in monoculture and mixture at the end of the 1982 growing season (August 2). Each bar is the mean of four observations (± 1 SE). Different letters indicate significant ($p < .05$) differences at each date by ANOVA.

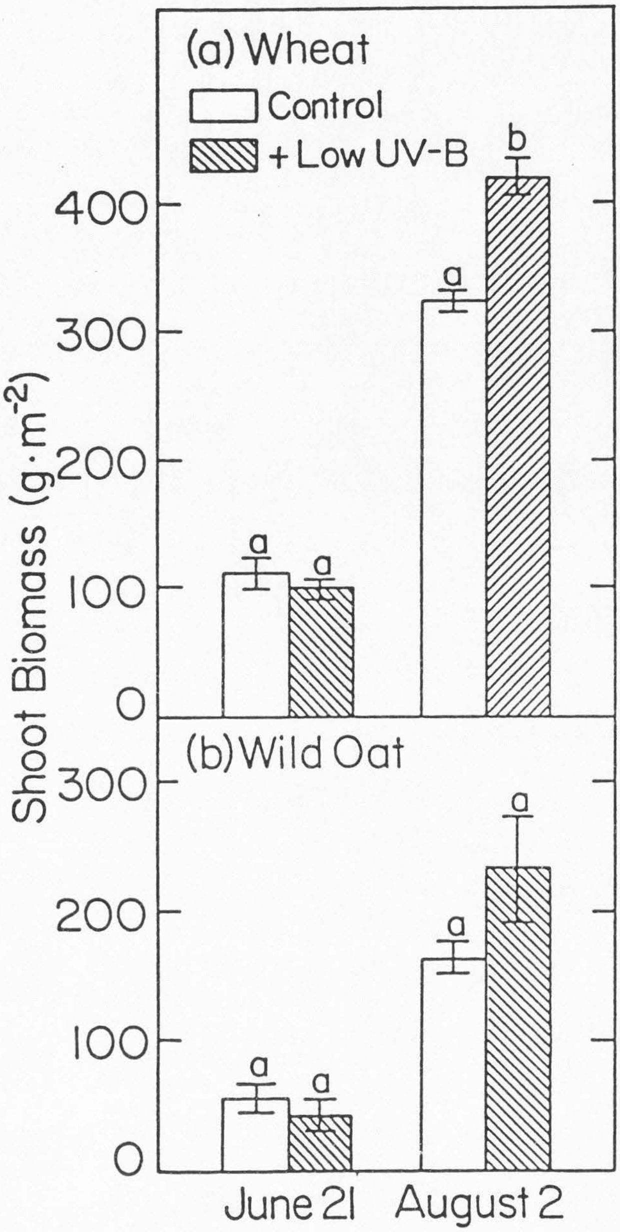


Figure 12. Shoot biomass production of wheat (a) and wild oat (b) monocultures in the water stress reduction plots during the 1982 growing season. Each bar is the mean of four observations (± 1 SE). Different letters indicate significant ($p < .05$) differences within species at each date by ANOVA.

the biomass increase seen in unwatered wild oat monocultures under high UV-B enhancement on August 2. Watered wheat monocultures under UV-B enhancement did not exhibit the same biomass depression relative to the control plots as the unwatered plots under UV-B enhancement on June 21 (Fig. 6).

UV-B enhancement apparently increased the relative crowding coefficients for total shoot biomass at the end of the growing season in the watered plots (Table 7) but this was not statistically significant. A similar pattern was seen in the relative crowding coefficients based upon reproductive production (Table 7). This was also found in the unwatered plots for 1982 (Table 4).

In contrast to the unwatered plots the total mixture plot biomass production for the watered plots was significantly affected by low UV-B enhancement (Fig. 13). However, this effect was not consistent for the two dates. On June 21 UV-B enhancement depressed total mixture plot production, while UV-B enhancement increased it on August 2.

On August 2 the relative yield total increased in the watered plots under UV-B enhancement (Table 7). This suggested a decreased competitive overlap for watered wheat/wild oat mixtures under low UV-B enhancement late in the growing season. This pattern was not evident in the unwatered wheat/wild oat mixtures on August 2. On June

Table 7. Relative crowding coefficients (k_{12}) and relative yield totals (RYT) based upon total shoot biomass and reproductive biomass for wheat/wild oat mixtures in water stress reduction plots during the 1982 growing season.

Competition Parameter	UV-B Treatment	June 21 Shoot Biomass*	August 2 Shoot Biomass*	August 2 Reprod. Biomass*
Relative Crowding Coefficient (k_{12})	Control	1.38^a	1.49^a	1.56^a
	Low Enhancement	1.29^a	1.65^a	1.82^a
Relative Yield Total (RYT)	Control	1.18^a	0.86^a	-
	Low Enchancement	1.02^a	1.10^b	-

*Different letters indicate significant ($P<.05$) differences within a column for each competition parameter by Student's t-test. Each value is the mean of four observations.

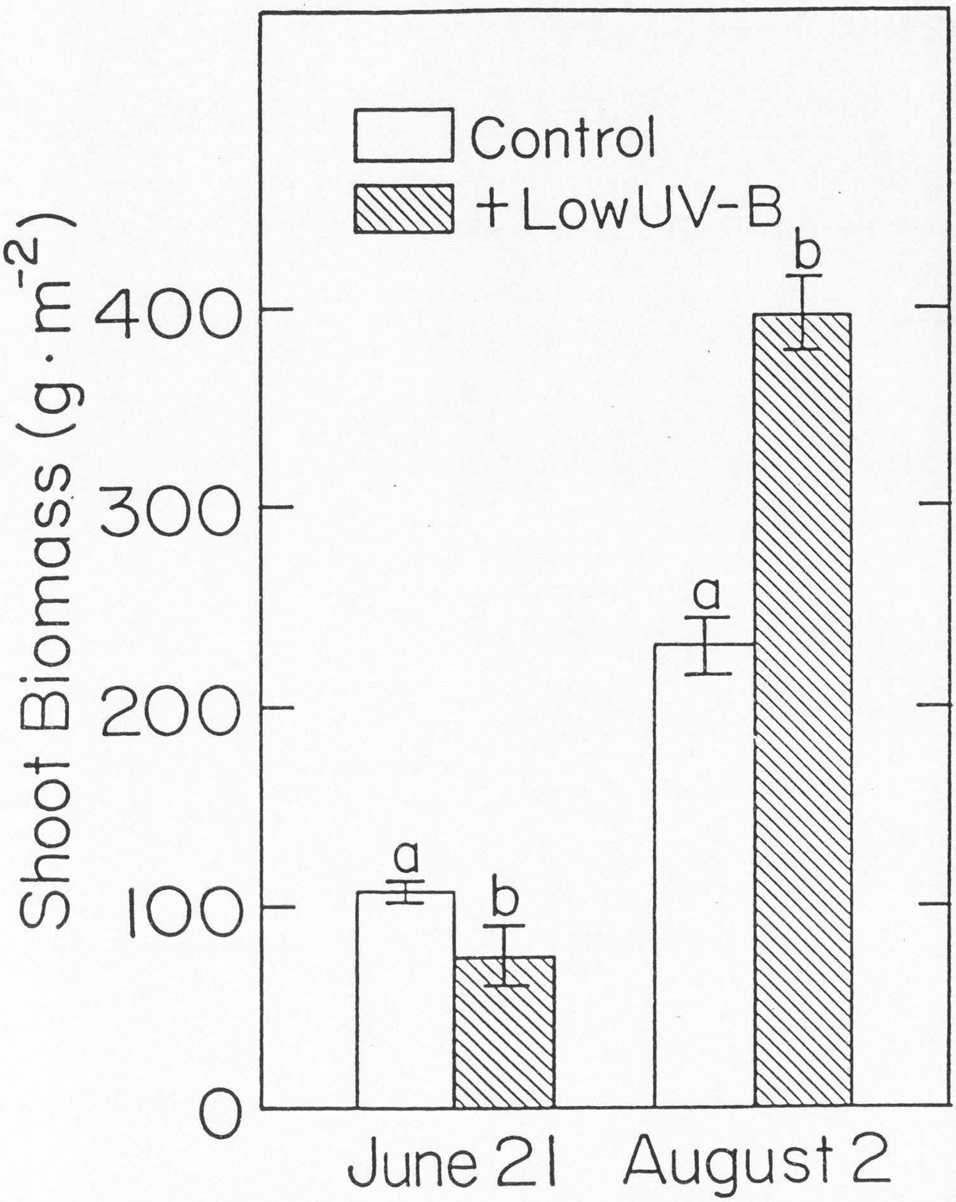


Figure 13. Total shoot biomass production of wheat/wild oat mixtures in the water stress reduction plots during the 1982 growing season. Each bar is the mean of four observations (± 1 SE). Different letters indicate significant ($p < .05$) differences at each date by ANOVA.

21, UV-B enhancement did not significantly affect the relative yield total in the watered plots (Table 7).

Fractional reproductive allocation of wheat or wild oat was not significantly affected by low UV-B enhancement in both monoculture and mixture in watered plots (Fig. 14). However, for both mixtures and monocultures there was a significant increase in fractional reproductive allocation for wild oat in the watered plots (average = 0.46) as compared to the unwatered plots (average = 0.31). This is probably a result of water being more limiting during reproductive production (later in the growing season) than during vegetative production. A significant increase in fractional reproductive allocation also existed for wheat in watered mixtures as compared to unwatered mixtures. However, this was not true for wheat monocultures.

The harvest index, a common agronomic measure, is the ratio of grain weight to total aboveground plant dry weight (Table 8). Although there are some small statistically significant differences in the low UV-B treatments relative to the controls, these differences appear biologically negligible. The reduction of water stress results in a substantial increase in the harvest index of all treatments. Once again, water is probably much more limiting during the later part of the season, when grain filling is taking place, than earlier, when more of the vegetative production is ocurring.

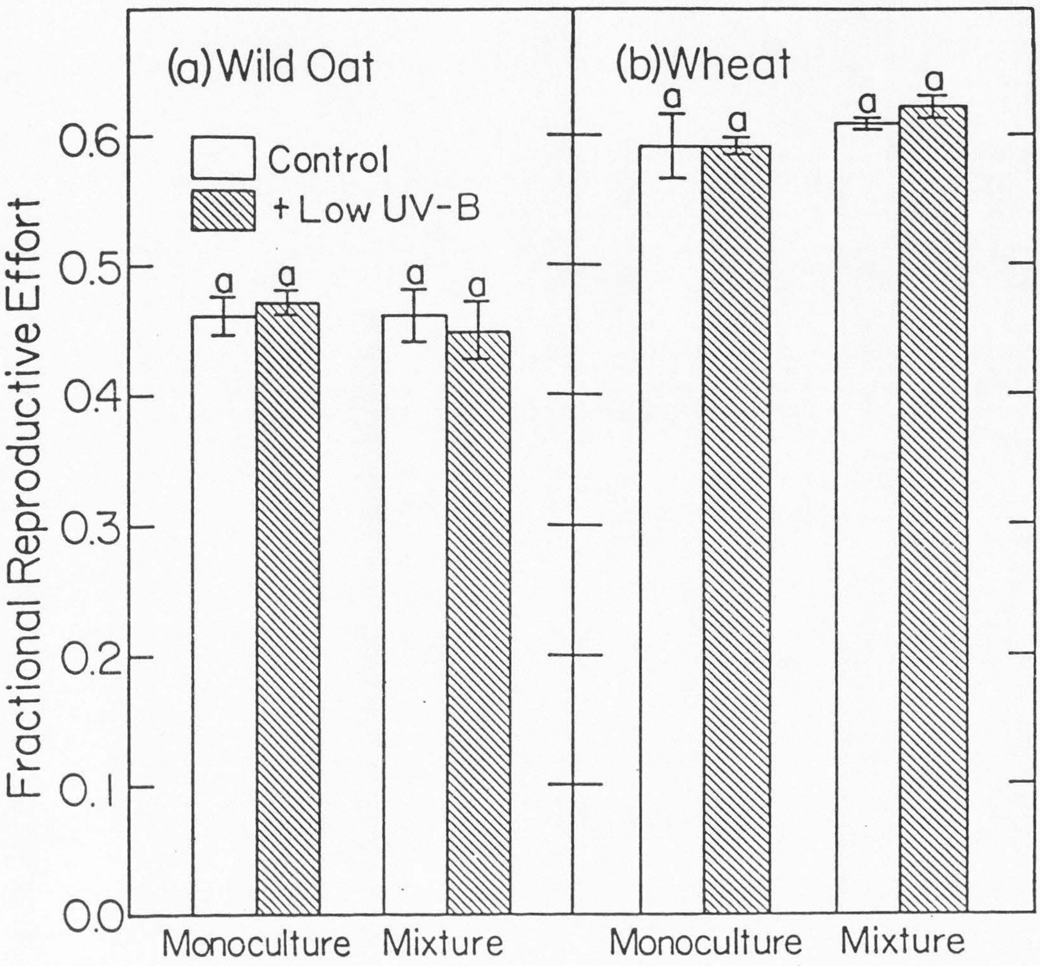


Figure 14. Fractional reproductive effort of wild oat (a) and wheat (b) in monoculture and mixture in the water stress reduction plots at the end of the 1982 growing season (August 2). Each bar is the mean of four observations (± 1 SE). Different letters indicate significant ($p < .05$) differences within species by ANOVA.

Table 8. Harvest index analysis for wheat at the end of the 1982 growing season.

Treatment	Total Wt. (g/m^2)*		Grain Wt. (g/m^2)*		Harvest Index**	
	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture
Control	18.0	9.4	7.27	3.97	0.40^{ab}	0.42^{bc}
+ Low UV-B	18.4	9.6	7.33	3.75	0.40^{ab}	0.39^{a}
+ High UV-B	16.8	10.3	6.73	4.32	0.40^{ab}	0.40^{ab}
Control (W)	25.7	12.9	11.10	5.34	0.44^{c}	0.44^{c}
+ Low UV-B (W)	32.8	22.4	14.07	10.17	0.43^{c}	0.46^{d}

*Each value is the mean of four observations.

**Different letters indicate significant ($P < .05$) differences within a column.

(W) indicates data from the water stress reduction experiment.

DISCUSSION

The current understanding of mechanisms of UV-B action upon plants suggests that UV-B irradiation should usually be detrimental (Caldwell 1981). However, some species may benefit indirectly from UV-B radiation and show increased biomass because of the depression of competing species more sensitive to UV-B (Fox and Caldwell 1978). Although the production of UV-B sensitive species may decrease under UV-B enhancement, the overall productivity of a plant community could be maintained by a consequent increase in production by less sensitive competing species. Thus, an increase in UV-B could alter the competitive interactions among plant species in an ecosystem without substantially changing the overall primary productivity (Fox and Caldwell 1978). Such a situation is unlikely in plant communities where competition is of little importance. In agricultural systems weedy competitors sometimes reduce the productivity of cultivated species and often reduce the quality of the harvested species. Differential sensitivity and response of these weeds and crop species to an increased UV-B environment could lead to substantial changes in the competitive situation and hence, to changes in the production and quality of the cultivated species.

Despite recent criticisms (Inyoue and Schaffer 1981), the deWit (1960) replacement series model is useful for examining competitive interactions in agricultural situations, where overall densitv is relatively constrained. The competitive interactions in this study were primarily examined with relative crowding coefficients. The relative crowding coefficients were calculated on the basis of two separate parameters, which reflect two different aspects of the competitive situation: total aboveground biomass and reproductive biomass. Crowding coefficients for total aboveground biomass reflect the relative ability of the species to use their limited resources, whereas crowding coefficients for reproductive biomass reflect the relative ability of the annual species to persist in future generations.

In wheat/wild oat mixtures the crowding coefficients for total aboveground biomass were significantly altered by UV-B supplementation. However, this effect was not consistent between the two years. In 1981 UV-B depressed the competitive ability of wheat; however, in 1982 UV-B enhanced the competitive ability of wheat. The difference in sowing dates could have been responsible for these conflicting results. In 1982 the plots were seeded in early May, when initial water status, temperature, and ambient ultraviolet radiation conditions were more favorable for plant growth and establishment than in the late June planting of 1981. The initial conditions for plant establishment significantly influence seedling development and, therefore, could have affected the relative ability of species to withstand increases in certain environmental stresses (such as UV-B radiation). Since spring wheat is usually sown in April in northern

Utah, the planting in 1982 was probably more agriculturally realistic and may be more representative of cultivated field situations. When seedlings of wheat/wild oat mixtures were exposed to more favorable establishment conditions, wheat apparently had a superior ability to withstand the damaging effects of increased UV-B radiation. However, when these seedling mixtures were exposed to high ambient UV-B flux, high air temperatures, and rapidly increasing water stress, wild oat was apparently less sensitive to increased UV-B radiation than wheat. This may reflect the higher degree of plasticity present in wild oat under harsher environmental conditions. Thus, temporal variability in environments could change the nature of competitive interactions and hence, the impact of a UV-B enhancement upon those interactions. The nature of the entire stress complex during the young life stages of competing species may be especially critical in determining the effect of increases in UV-B on interspecific competition.

In 1982 reproductive production in wheat/wild oat mixtures exhibited the same pattern as total aboveground biomass. Thus, based on 1982 data, wheat had an increased competitive ability under increased UV-B radiation, both in terms of its ability to use available resources for current biomass production and to allocate resources to the reproductive effort.

In 1982 the reduction of water stress in the wheat/wild oat mixtures resulted in a loss of the significant UV-B enhancement effect on the relative crowding coefficients of wheat with respect to wild oat that was evident in the unwatered plots. Thus, water stress apparently exacerbated the effect of UV-B stress upon wheat/wild oat competitive interactions.

In 1981 the competitive ability of wheat in wheat/jointed goatgrass mixtures was increased under enhanced UV-B conditions. This was opposite to the reponse obtained in 1981 for the wheat/wild oat mixtures. Thus, the competitive response of wheat under increased UV-B conditions was highly dependent upon which particular species was in competition with it.

The overall competitive situation, as reflected by the relative yield totals, did not show any consistent effect of increased UV-B radiation on the degree of competitive overlap present in the mixtures. Increased UV-B apparently did not affect the degree to which species made demands upon the same resources. In addition, total biomass production of mixture plots was not affected by UV-B enhancement in both 1981 and 1982. Thus, although the competitive interactions of these mixtures were significantly altered by an enhanced UV-B environment, both the degree of competitive overlap and total mixture plot production were unaffected by UV-B enhancement in either year of the study. This supports the idea that increased UV-B radiation may alter the competitive interactions of a system, rather than decrease total system production (Fox and Caldwell 1978). The degree of competitive overlap is dictated by the particular morphological and physiological attributes of the species which determine their particular resource demands. Hence, these results are probably specific to these particular species pairs (and wheat cultivar). When water stress was reduced, UV-B enhancement resulted in a reduced competitive overlap for wheat/wild oat mixtures late in the growing season. This suggested that general plant characteristics determining resource use were altered by UV-B enhancement only when water stress was reduced. Thus, the response of competing plant species to increased UV-B radiation was dependent upon the degree of water stress present and may have been constrained at higher levels of water stress.

Under enhanced UV-B conditions the fractional reproductive effort of wild oat was decreased in mixtures. This may be the result of a greater flexibilty in this weedy species than wheat for allocating resources to vegetative versus reproductive production. This pattern was in contrast to wheat where the fractional reproductive effort was apparently not affected by any stress. This reduction in fractional reproductive effort by wild oat suggests a diversion of more resources to vegetative processes to deal with a high degree of water stress and enhanced UV-B stress. This allocation change may be necessary to help wild oat maintain a more favorable competitive status in the mixture under high water stress.

Wild oat is an agricultural weed that has evolved under a high degree of competitive pressure in a relatively optimal environment. Therefore, its adaptive response may be one of maintaining vegetative production at the expense of some reproductive effort. This may be necessary to maintain a viable, competitive position, which is necessary for at least some successful reproduction. This situation may be quite different for ruderal weedy species, where competitive pressure is low and fast, maximal reproductive output will allow the rapid colonization of a site. However, this alteration of fractional reproductive allocation could simply represent a significant inhibition of photosynthate production in the flag leaf (the major source of photosynthate for grain filling) under enhanced UV-B rather than a high degree of flexibility in allocation. High water stress and interspecific competition may prevent the wild oat plants from compensating for this UV-B inhibition. In fact, when water stress was reduced in this study wild oat did not show a decrease in fractional reproductive allocation under UV-B enhancement in mixtures. The constant fractional reproductive effort of wheat indicated a small degree of plasticity, which would be expected in a highly selected, agronomic species.

Although the major focus of this study dealt with the effects of increased UV-B on the competitive interactions of species pairs, the response of each species in monospecific stands is also of interest (see Objective 2). The effects of increased UV-B radiation on monoculture stands are useful both as a baseline to compare the effect of increased UV-B on mixtures and in revealing individual species response in isolation from interspecific competition. In this study no consistent relationship was found between the level of UV-B radiation and monoculture biomass production. A significant depression in wheat biomass exsisted at the beginning and middle of the 1982 growing season, but the low UV-B enhancement apparently depressed production more than the high UV-B enhancement. Also, this depression was not evident by the end of the growing season. Apparently UV-B stress only affected monocultures early in the season. Although many environmental factors change through the growing season, one of the most important is the increase in water stress as the season progresses. The disappearance of this UV-B effect late in the season could be attributed to a large increase in the effects of water stress, resulting in a masking of the UV-B effects. However, when water stress was reduced in some plots there was no detectable effect of UV-B upon monoculture production at any time of the season. Thus, water stress did not mask the effects of UV-B stress on biomass production in monoculture at the end of the growing season. All of the results of this study are summarized in Table 9 with regard to the specific hypotheses presented earlier.

Table 9. Summary of the results of this study with regard to the hypotheses presented earlier.

Hypothesis	Summary of Results
H1a.	The competitive interactions of wheat/wild oat and wheat/jointed goatgrass mixtures were altered by UV-B enhancement in 1981 and 1982.
H1b.	Total mixture plot production was not affected by enhanced UV-B radiation.
H2.	UV-B enhancement did not clearly affect monoculture production of biomass in the three species. The only significant effect was a depression of wheat production early in the 1982 growing season.
H3.	UV-B enhancement did not affect biomass allocation to reproduction in wheat. However, wild oat exhibited a decrease in proportional allocation to reproduction under UV-B enhancement in mixture plots (not in monoculture plots).
H4.	No consistent effect of water stress upon the interaction between UV-B radiation and plant competition was found. Some data suggest that the depression of wheat monoculture production under UV-B enhancement was exacerbated by water stress. However, other data indicate that water stress masked an effect of UV-B enhancement on both total mixture plot production and competitive overlap of wheat/wild oat mixtures at one time. These are isolated cases and only serve to indicate that water stress does affect the interaction of UV-B and plant competition in some respects.

The agricultural implications of enhanced UV-B are not completely clear from these experiments. With enhanced UV-B wheat gained a competitive advantage over wild oat under realistic field conditions (1982). This implies that total grain yield and quality may actually be increased under enhanced UV-B because of the corresponding reduction of wild oat. Despite the competitive advantage gained by wheat under enhanced UV-B conditions, the relative proportion of aboveground biomass allocated to grain production (harvest index) remains the same. Thus, any agricultural advantages would come from increases in total wheat plant production and decreases in wild oat seed production and hence, cleaner grain. Although these experiments were conducted under relatively realistic field conditions, caution must be used in extrapolating to agricultural situations. Different environmental conditions and/or different plant species may yield other results. Also, as Haizel and Harper (1973) emphasize, agricultural crops grow against a background of many weedy species. Consequently, it is impossible from the present study to predict the response of those other species to both the direct increase in UV-B radiation and the reduction in competitiveness of wild oat. Although this multiple species approach is more realistic, the prominence of wild oat in the weed communities of most wheat fields suggests that the two species approach used in the present study may be applicable in a number of field situations.

LITERATURE CITED

Austin, M.P., and B.O. Austin. 1980. Behaviour of experimental plant communities along a nutrient gradient. J. Ecol. 68: 891-918.

Becwar, M.R., F.D. Moore III., and M.J. Burke. 1982. Effects of deletion and enhancment of ultraviolet-B (280-315 nm) radiation on plants grown at 3000 m elevation. J. Amer. Soc. Hort. Sci. 107: 771-774.

Biggs, R.H., W.B. Sisson, and M.M. Caldwell. 1975. Response of higher terrestrial plants to elevated UV-B irradiance. Pages 4-34 - 4-50 in D.S. Natchway, M.M. Caldwell, and R.H. Biggs, eds. Impacts of Climatic Change on the Biosphere. Climatic Impact Assessment Program Monograph 5. Report Number DOT-TST-75-55. United States Department of Transportation, Springfield, VI.

Biggs, R.H., and S.V. Kossuth. 1978. Impact of solar UV-B radiation on crop productivity. Final Report of UV-B Biological and Climate Effects Research, Non-human Organisms. U.S. Environmental Protection Agency Report No. EPA-IAG-D6-0618. Washington D.C.

Bjorkman, O. 1981. Ecological adaptation of the photosynthetic apparatus. Pages 191-202 in G. Akoyunoglou, ed. Photosynthesis VI. Photosynthesis and Productivity, Photosynthesis and Environment. Balaban Intl. Science Services, Philadelphia, PA.

Bogenrieder, A., and R. Klein. 1982. Does solar UV influence the competitive relationship in higher plants?. Pages 641-649 in J. Calkins, ed. The Role of Solar Ultraviolet Radiation in Marine Ecosystems. Plenum Press, New York. 724 pp.

Brown, D.A. 1955. Effects of competition of wild oats on yields of wheat. NCWCC Research Report 12: 1-58.

Caldwell, M.M. 1968. Solar ultraviolet radiation as an ecological factor for alpine plants. Ecol. Monogr. 38: 243-268.

Caldwell, M.M. 1971. Solar ultraviolet radiation and the growth and development of higher plants. Pages 131-177 in A.C. Giese, ed. Photophysiology Volume 6. Academic Press, New York. 388 pp.

Caldwell, M.M. 1981. Responses to solar ultraviolet radiation. Pages 169-198 in O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds. Physiological Plant Ecology: Responses to the Physical Environment. Encyclopedia of Plant Physiology, new series, volume 13A. Springer-Verlag, New York. 625 pp.

Caldwell, M.M., W.G. Gold, G. Harris, and C.W. Ashurst. 1983. A modulated lamp system for solar UV-B (280-320 nm) supplementation studies in the field. Photochem. Photobiol. in press.

deWit, C.T. 1960. On competition. Versl. Landbowk. Onderzoek. The Hauge. 66: 1-82.

Fox, F.M., and M.M. Caldwell. 1978. Competitive interaction in plant populations exposed to supplementary ultraviolet-B radiation. Oecologia. 36: 173-190.

Green, A.E.S., K.R. Cross, and L.A. Smith. 1980. Improved analytic characterization of ultraviolet skylight. Photochem. Photobiol. 31: 59-65.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Grime, J.P. 1979. Plant Strategies & Vegetation Processes. John Wiley & Sons, New York. 222 pp.

Haizel, K.A., and J.L. Harper. 1973. The effects of density and the timing of removal on interference between barley, white mustard and wild oats. J. Appl. Ecol. 10: 23-31.

Harm, W. 1979. Relative effectiveness of the 300-320 nm spectral region of sunlight for the production of primary lethal damage in E. colli cells. Mutation Res. 60: 263-270.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York. 892 pp.

Henson, J.F., and L.S. Jordan. 1982. Wild oat (Avena fatua) co petition with wheat (Triticum aestivum and T. turgidum durum) for nitrate. Weed Sci. 30: 297-300.

Inouye, R.S., and W.M. Schaffer. 1981. On the ecological meaning of ratio (deWit) diagrams in plant ecology. Ecology 62(6): 1679-1681.

Lee, T.D., and F.A. Bazzaz. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant Abutilon theophrasti. J. Ecol. 68: 813-821.

Lipton, W.J., and J.J. O'Grady. 1980. Solar injury of "Crenshaw" muskmelons: the influence of ultraviolet radiation and of high tissue temperatures. Agric. Meteorol. 22: 235-247.

Martin, J.H., W.H. Leonard, and D.L. Stamp. 1976. Principles of Field Crop Production. 3rd ed. Macmillan Publ. Co. New York.

McWhorter, C.G., and D.T. Patterson. 1980. Ecological factors affecting weed competition in soybeans. Pages 371-392 in F.T. Corbin, ed. World Soybean Research Conference II : Proceedings. Westview Press, Boulder, CO.

Mueggler, W.F. 1972. Influence of competition on the response of bluebunch wheatgrass to clipping. J. Range Manage. 25: 88-92.

National Academy of Sciences. 1979. Protection Against Depletion of Stratospheric Ozone by Chlorofluorocarbons. National Academy Press, Washington D.C. 392 pp.

National Academy of Sciences. 1982. Causes and Effects of Stratospheric Ozone Reduction : An Update. National Academy Press, Washington D.C. 339 pp.

Rothman, R.H., and R.B. Setlow. 1979. An action spectrum for cell killing and pyrimidine dimer formation in Chinese hampster V-79 cells. Photochem. Photobiol. 29: 57-62.

Sisson, W.B., and M.M. Caldwell. 1975. Lamp/filter systems for simulation of solar UV irradiance under reduced atmospheric ozone. Photochem. Photobiol. 21: 453-456.

Teramura, A.H., R.H. Biggs, and S.V. Kossuth. 1980. Effects of ultraviolet-B irradiance on soybean. II. Interaction between ultraviolet-B and photosynthetically active radiation on net photosynthesis, dark respiration and transpiration. Plant Physiol. 65: 483-488.

Tingey, D.C. 1965. Control of wild oats in small grains. Utah State University Ag. Expt. Stat. Bull. No. 450. Logan, Utah.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall Inc. Englewood Cliffs, New Jersey. 620 pp.